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IN THE
SNAKE RIVER
BIRDS OF PREY AREA

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FINAL REPORT

ECOLOGY OF REPTILES IN THE SNAKE RIVER BIRDS OF PREY NATURAL AREA

Submitted by

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ABSTRACT

Line-transect censusing of lizard densitites indicate that shadscale (*Atriplex confertifolia*), talus and canyon rim habitats yield the highest density estimates. Because of their body size, abundance and widespread distribution, western whiptail lizards (*Cnemidophorus tigris*) were found to have the greatest potential as a prey species for raptors. Lizard seasonal activity typically begins in April, reaches a peak by early June, drops off during July and August and then reaches a small secondary peak in October after which all activity ceases. Daily activity of lizards reaches a peak at midday during cool spring weather. In summer, most lizards have a bimodal activity pattern with peaks of activity in late morning and evening.

Gopher snakes (*Pituophis melanoleucus*) and western rattlesnakes (*Crotalus viridis*) were the two most frequently captured snake species. However, density estimates derived from a drift fence census indicate that night snakes (*Hypsiglena torquata*) and gopher snakes are the most abundant snakes with densities of 1.4 and 1.3 snakes/ha, respectively. Although not as abundant, western rattlesnakes followed gopher snakes closely in biomass estimates due to their larger body size. Rocky habitats such as the canyon rim and talus slopes had the highest density of snakes. Most snake activity began in late April, reached a peak during the last of May and the first of June and gradually diminished throughout summer with no secondary peak in the fall. Snake species showed considerable individual variation in daily activity patterns. Three snake species investigated (western rattlesnakes, gopher snakes and striped whipsnakes, *Masticophis taeniatus*) all had preferred body temperatures of about 30° C. Studies of snake movements indicate that most snakes in the study area do not have home ranges in the traditional sense, but wander over relatively large areas in a somewhat random fashion. Five size classes of western rattlesnakes and gopher snakes and four size classes of striped whipsnakes could be identified using length-frequency curves. These length-frequency curves also indicate that all three snake species are relatively long-lived with high mortality in the younger age classes and low mortality as adults. Growth rates were estimated from recapture data, growth of captive held snakes and increase in size between age classes. The latter approach gave the best results. Most female rattlesnakes and gopher snakes reproduce for the first time in their fourth summer, while males have sperm in their efferent

ducts by the fall of their second and third summers, respectively, for western rattlesnakes and gopher snakes. Mean clutch size for 33 western rattlesnakes was 8.3, and 21 gopher snakes had a mean clutch of 6.5 eggs. Female gopher snakes reproduce annually, while 75% of the sexually mature female rattlesnakes reproduce annually. Rattlesnakes have the highest percent body fat followed by gopher snakes and striped whipsnakes. In all three species, females usually have higher percent body fat than males. Fat reserves are utilized mainly for reproduction in these snakes.

Over 80% of a western rattlesnake's diet consists of Townsend ground squirrels (Spermophilus townsendi), while gopher snakes mainly feed on a variety of small mammals. Striped whipsnakes have a highly varied diet which includes lizards, small mammals and other snakes. Feeding studies done with western rattlesnakes and gopher snakes indicate that rattlesnakes have a higher consumption rate and growth (production) efficiency than do gopher snakes. Based on density estimates, food habits and consumption rates, western rattlesnakes consume 2.3 Townsend ground squirrels per hectare on the average, but in some areas of preferred rattlesnake habitat, 25 ground squirrels per hectare may be taken. Because of their more generalized diet, gopher snakes do not take a significant number of any one prey species. A drought in 1977 caused a drastic reduction in feeding, early cessation of activity, reduced body weight and a decrease in reproductive output for rattlesnakes. Gopher snakes showed no major response to the drought.

INTRODUCTION

A variety of raptors are known to take reptiles as prey. Golden eagles, prairie falcons and red-tailed hawks, which are probably the three most abundant nesting species in the Snake River Birds of Prey Natural Area, all take at least some snakes and lizards (USDI 1979). Thus, this study was initiated to determine species composition and biomass of snakes and lizards in various habitats/cover types within the Birds of Prey study area. These data would be used to assess the potential of various reptile species as prey for raptors.

During the early phases of this study it also became apparent that western rattlesnakes and gopher snakes take many of the same mammalian prey as do certain raptors. These snakes served as both prey and potential competitors with raptors in the study area. Thus, a second objective of this study was to determine the impact of rattlesnakes and gopher snakes on prey populations that are also utilized by raptors.

Finally, since much of the land within the Birds of Prey Natural Area is threatened with agricultural development (USDI 1979), a third objective was to determine the effects of habitat alteration on reptile densities.

STUDY AREA

This study was conducted from 1975-79 within the 338,778 ha Birds of Prey Study Area (BPSA) in southwest Idaho (Fig. 1). The area is relatively dry with a mean annual precipitation of 20 cm. Summers are characterized by hot days and cool nights. The overall mean temperature for July is about 24°C. Winters are relatively mild with a January mean temperature of about -2°C.

A major topographic feature of the BPSA is the Snake River canyon. At its deepest points, the elevation of the canyon ranges from 700 m at river level to 920 m at the rim with vertical cliffs up to 125 m. North of the river the soils are formed from loess deposits and tend to be deep. Big sagebrush (*Artemisia tridentata*) and winterfat (*Ceratoides lanata*) are the most common shrubs with abundant grasses (mainly cheatgrass, *Bromus tectorum* and Sandberg bluegrass, *Poa sandbergii*). South of the river the soils are typified by lacustrine deposits of sand, gravel and silt, which supports mainly shadscale (*Atriplex confertifolia*) and greasewood (*Sarcobatus vermiculatus*). Most of the land within the BPSA is grazed by livestock, and considerable agricultural development occurs within or adjacent to the BPSA. Accessible portions of the canyon are popular recreational areas (USDI 1979).

METHODS

Lizard densities were estimated during the seasonal activity peak (May & June) using an observational strip-census technique (Degenhardt 1966). Two to three transects of varying lengths were established in each of the major cover types (Fig. 1). Each transect was walked at least twice in both morning and evening to ensure censusing during the daily activity peak of each lizard species. Transect lengths were adjusted to the maximum distance that could be covered during a daily activity peak (2-3 hours). The area censused for each lizard species was computed by multiplying the transect length by twice the average maximum perpendicular distance of detection from the transect line. The density index for each species was calculated as the maximum number of individuals encountered during any one effort, divided by the area censused. Whenever possible, lizards encountered were captured and measurements were taken to determine biomass.

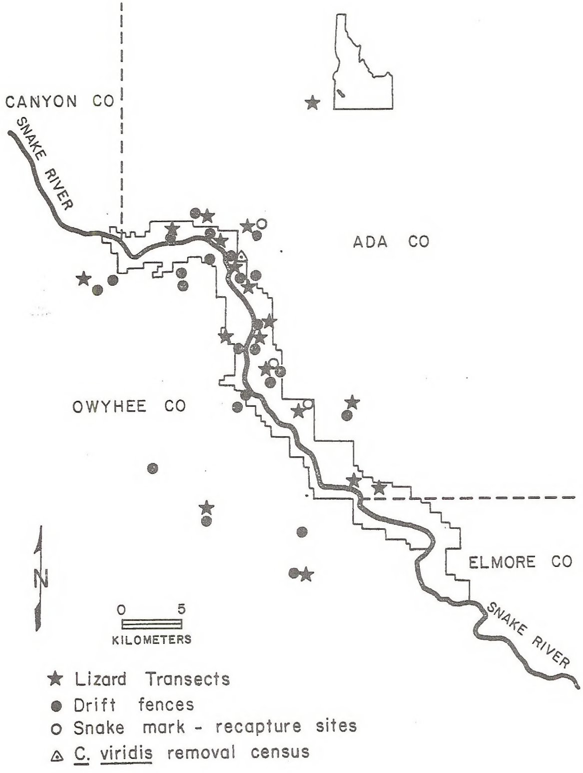


Fig. 1. Locations of lizard transects, drift fences, snake mark-recapture sites and rattlesnake removal census within the BPSA.

Snake densities were estimated by several means. At certain sites with high snake densities, mark-recapture studies were conducted (Fig. 1). Snakes were permanently marked by applying a heat brand to their ventral scales. However, only western rattlesnakes were recaptured frequently enough to estimate density using this method. Their density was determined by intensively searching an area for several days marking snakes, until all rattlesnakes were marked. Then, total number marked was considered a minimum population estimate. At another site, western rattlesnake density was estimated by a removal census (Fig. 1). The site was searched intensively over a period of nine days until no more rattlesnakes could be found. Total number removed was considered a minimum population estimate.

All other snake densities were estimated from the number of captures in drift fences. In 1977, four drift fences were erected to test their feasibility in censusing snake densities. Then in 1978 on the north side, and in 1979 on the south side of the Snake River, twelve drift fences were erected in a total of nine major habitat types (Fig. 1). Each drift fence consisted of a 30 m section of galvanized metal 51 cm high with two "snake traps" located 7.6 m from each end. The "snake traps" are boxes constructed out of 3.2 mm (1/8 inch) hardware cloth, which are 1.2 m long by 0.6 m wide and 0.3 m high, with funnels leading into the trap from both ends. The traps are located at breaks in the "fence", so that snakes attempting to get around the barrier from either side will be funneled into the trap. Captured snakes were marked, sexed, weighed and measured, and then released 20-30 m from the drift fence. The drift fences also captured various mammals, birds, amphibians, lizards and invertebrates (see Appendix A).

To better define snake movements, home range, and the best method for converting drift fence captures into density estimates, some snakes captured in drift fences in 1979 were tagged with radioactive tantalum (^{182}Ta). In all, 22 snakes of 5 different species were tagged with a maximum of 400 μCi in the form of a thin wire inserted under the skin of the tail. These snakes were then released, and their activities were monitored with the aid of a Geiger-Muller counter. Tagged snakes could be detected at 4 m on the surface and through about 0.5 m of packed soil. The results of this tagging study indicate that most snakes in the BPSA do not have a distinct home range, but instead, wander over relatively large areas in a somewhat random fashion. Thus snake movements are assumed to be random in relation to a drift fence, so that the area censused by a drift fence for a given snake species is equal to the effective trapping width of the drift fence multiplied by the mean total distance which that snake species would move during the trapping period. Movement rates were estimated for the western rattlesnakes using our own mark-recapture data. Movement rates for all other snakes came from the following sources: McNab 1963, Barbour et al., 1969, Hirth et al. 1969, and Parker 1974. Whenever sufficient recaptures occurred, home ranges of western rattlesnakes were determined using the convex polygon method (Jennrich and Turner 1969).

The following information was recorded for most snakes that were captured and released: date, time, sex, snout-vent length, body weight, cloacal, air and substrate temperatures, location and cover type/substrate in which the snake was found. Some snakes were collected and frozen for later dissection. The data derived from dissections were: fat body weight, reproductive conditon and prey items in gut.

In addition to the data derived from dissections, snake food habits were determined by three other methods. All snakes with prey in their stomachs were palpated. Scats were collected from snakes by keeping the snakes in collecting bags for several days. Snakes scats were also collected in the field. The only remains of mammalian prey in snake scats were hair, which was identified to species in most cases with the aid of a hair-key (Moore et al. 1974).

Consumption rates and growth efficiencies of gopher snakes (Pituophis melanoleucus) and western rattlesnakes were determined by conducting feeding studies of captive snakes. These snakes were maintained in outdoor enclosures during the summer months, and were fed known amounts of their natural prey items. The snakes were offered food frequently, so that they could feed ad libitum. Consumption rate was calculated as a percent of the snake's body weight of prey that was consumed per day, and growth efficiency was calculated by dividing the total weight of all the prey consumed during the feeding period by the total weight gain of the snake.

RESULTS AND DISCUSSION

Body Weights of BPNA Reptiles

Cumulative data on body weights for 1975 through 1978 are listed in Table 1. Since virtually every snake encountered was weighed, the N value

Table 1. Mean body weights of snakes and lizards collected in the BPSA.

Species	All Age Classes n	x̄ (g)	SD	Excluding Young N	x̄ (g)	SD
Lizards						
Western whiptail (*Cnemidophorus tigris*)	44	15.4	5.84	39	17.0	3.91
Collared (*Crotaphytus collaris*)	23	28.3	13.67	18	34.2	8.22
Leopard (*Gambelia wislizenii*)	38	22.8	7.92	31	25.6	5.47
Desert horned (*Phrynosoma platyrhinos*)	77	17.8	9.08	42	23.6	6.12
Western fence (*Sceloporus occidentalis*)	44	16.9	5.03	40	18.1	3.60
Side-blotched (*Uta stansburiana*)	69	3.6	0.93	--	--	--
Snakes:						
Gopher (*Pituophis melanoleucus*)	405	201.8	126.95	355	226.5	115.33
Western rattlesnake (*Crotalus viridis*)	352	392.7	195.15	319	424.9	174.59
Striped whipsnake (*Masticophis taeniatus*)	246	102.3	50.51	223	111.4	43.95
Night (*Hypsiglena torquata*)	52	14.4	8.28	45	15.4	8.37
Longnose (*Rhinocheilus lecontei*)	35	73.1	31.95	29	84.7	20.56
Western ground (*Sonora semiannulata*)	31	7.9	2.61	26	8.6	2.15
Racer (*Coluber constrictor*)	24	77.2	40.83	--	--	--
Western terrestrial garter (*Thamnophis elegans*)	8	109.0	64.89	--	--	--

for each snake species also reflected its relative abundance, allowing for certain biases due to activity patterns and detectibility. The N value for lizard species in no way reflected their relative abundance, since lizards were captured for measurements in a subjective manner.

Lizard Density and Biomass

The results of the observational lizard strip-census are listed in Table 2. The data indicate that the habitat with the greatest lizard biomass is talus slope, but the diversity of lizard species there was low. Canyon rim and shadscale (*Atriplex confertifolia*) habitats, respectively, gave the next two highest biomass estimates, and they also had the greatest diversity of lizard species. Considering the relative proportion of each to the total area of the BPSA (USDI 1979), shadscale and canyon rim habitats probably contain the greatest total biomass of lizards. Greasewood (*Sarcobatus vermiculatus*) and riparian habitats produced moderate biomass estimates with winterfat (*Ceratoides lanata*), big sage (*Artemisia tridentata*) and grass giving the lowest estimates. The one consistent characteristic is that habitats with high lizard densities have relatively low percent vegetative cover with many areas of open ground or rocks. Areas of low lizard densities have high percent vegetative cover and little or no open ground.

Relative Importance of Lizard Species in the BPNA

Side-blotched lizards (*Uta stansburiana*) are the most abundant lizards in the BPSA (Table 3). They are also widespread, but because of their small size they probably are not an important prey species. The lizard with the greatest potential as a prey species is probably the western whiptail (*Cnemidophorus tigris*), since it is the most ubiquitous, and also has a relatively high mean biomass (g/ha). Western fence lizards (*Sceloporus occidentalis*) have the highest mean biomass values (Table 3) of any lizard, but their importance is reduced, since they occur only in a few restricted habitats. Leopard lizards (*Gambelia wislizenii*) are also a potentially important prey species, because they are rather widespread and have a large body size.

Lizard Seasonal Activity Patterns

Most lizard species were captured in the snake drift fences. Since greater activity increases the chance of a lizard being captured in a

Table 2. Indices of lizard density and biomass. C.t. = Western Whiptail (*Cnemidophorus tigris*); G.w. = Leopard Lizard (*Gambelia wislizenii*); C.c. = Collared Lizard (*Crotaphytus collaris*); U.s. = Side-blotched Lizard (*Uta stansburiana*); P.p. = Desert Horned Lizard (*Phrynosoma platyrhinos*); S.o. = Western Fence Lizard (*Sceloporus occidentalis*).

Habitat Type (grid coordinates)	Species	Density (n/ha)	Biomass (g/ha)	Transect Total	Mean Habit Biomass
Winterfat (a) (328875)	C.t.	0.6	8.5		
	G.w.	0.6	12.6		
	U.s.	2.7	9.8	30.8	
Winterfat (b) (314896)	C.t.	0.7	10.7		
	G.w.	0.3	7.8		
	U.s.	12.2	44.6	63.0	46.9
Big Sage (a) (320924)	G.w.	1.8	42.2		
	U.s.	2.8	10.1	52.3	
Big Sage (b) (297932)	C.t.	1.0	15.9		
	p.p.	1.0	18.3	34.2	
Big Sage (c) (308868)	C.t.	2.1	32.0		
	P.p.	2.5	44.2		
	U.s.	1.2	4.5	80.7	55.7
Shadscale (a) (371825)	C.t.	1.0	15.0		
	G.w.	0.6	14.8		
	P.p.	0.6	9.8		
	U.s.	11.1	40.3	79.9	
Shadscale (b) (385796)	C.t.	5.6	85.8		
	G.w.	0.4	9.1		
	P.p.	1.9	34.4		
	U.s.	14.2	51.6	180.8	
Shadscale (c) (303780)	C.t.	2.5	38.1		
	G.w.	1.9	42.4		
	P.p.	2.5	44.2		
	U.s.	9.9	36.2	160.9	140.5
Canyon rim (a) (328852)	C.t.	1.9	28.9		
	S.o.	1.2	21.2		
	U.s.	8.4	30.6	80.7	
Canyon rim (b) (348834)	C.c.	1.3	37.6		
	C.t.	2.0	30.9		
	P.p.	0.7	11.9		
	S.o.	2.7	45.2		
	U.s.	6.0	21.8	147.5	

Table 2. continued

Habitat Type (grid coordinates)	Species	Density (n/ha)	Biomass (g/ha)	Transect Total	Mean Habit Biomass
Canyon rim (c) (323873)	C.c.	0.6	16.7		
	C.t.	1.8	27.2		
	G.w.	1.2	26.9		
	S.o.	7.6	128.1		
	U.s.	8.2	30.0	228.9	152.4
Talus slope (a) (278921)	S.o.	9.5	161.3		
	U.s.	11.4	41.4	202.6	
Talus slope (b) (307904)	S.o.	8.5	144.5		
	U.s.	6.2	22.6	167.0	184.8
Riparian (a) (370795)	C.t.	6.4		99.5	
Riparian (b) (300913)	C.t.	2.2	34.1		
	S.o.	3.1	52.5	86.6	93.1
Greasewood (a) (224897)	C.t.	2.3	35.6		
	U.s.	2.8	10.1		
	G.w.	0.9	19.8	65.6	
Greasewood (b) (343752)	C.t.	5.7	87.8		
	G.w.	2.8	64.8		
	P.p.	0.9	16.9	169.5	117.6
Grass (Sand Creek)	0	0	0	0	0

Table 3. Relative Importance of Lizard Species in the BPSA.

Lizard Species	Percent Occurrence in Transects	*Mean Density (N/ha)	*Mean Biomass (g/ha)
Western Whiptail	78	2.5	39.3
Side-Blotched	72	7.5	27.2
Western Fence	33	5.4	92.1
Leopard	50	1.2	26.7
Desert Horned	39	1.4	25.7
Collared	11	1.0	27.2

*Mean values represent averages from the transects where the lizard species occurs.

drift fence, the frequency of lizard captures should reflect seasonal lizard activity (Table 4 and Fig. 2). These captures indicate that May and June are the months of greatest lizard activity, with activity dropping off rapidly in July and August. Fig. 2 indicates that the actual peak of lizard activity occurs during the last of May and the first of June. It is of interest to note that there is a secondary peak of activity in October, but it is due solely to side-blotched lizard activity. Also, the majority of these lizards are represented by young of the year. Since the drift fences were not in operation until the end of April, Table 4 and Fig. 2 do not indicate that in most years lizard activity begins in late March or early April depending on weather conditions.

Lizard Daily Activity and Thermal Preferences

Daily activity patterns of lizards in the BPSA were not directly monitored. However, numerous authors have established a bimodal daily activity pattern for most temperate lizards during the warm summer months, with a unimodal pattern observed in the cooler spring and fall days (Heath 1965; Tinkle 1967; Tanner and Krogh 1974; Pianka and Parker 1975; Parker and Pianka 1976). Fig. 3 indicates the daily activity pattern for the short horned lizard (Phrynosoma douglassi) in central Oregon (Diller 1973 - unpublished data). Most lizards in the BPSA could be expected to show this same type of activity pattern during the summer months, with the highest activity peak in mid-morning and a secondary peak in late afternoon. During cooler weather in the spring and fall, the two activity peaks would come together as a single peak during midday. In the BPSA, the only exception to this basic daily activity pattern is found in the western whiptail. It has a single activity peak in late morning or early afternoon throughout the entire season and usually is completely inactive during the late afternoon and evening (Burkholder and Walker 1973).

The daily activity patterns of lizards are mainly dependent on their need to maintain a desired body temperature. The lizards of the BPSA could be expected to show the same relationships between substrate, body and air temperatures as is seen in Fig. 4 for the short horned lizard in central Oregon (Diller 1973 - unpublished data). These curves indicate that a lizard can maintain a body temperature higher than air temperature and lower than substrate temperature. This is achieved by behavioral

Table 4. Seasonal lizard activity patterns as represented by monthly drift fence captures. C.t. = Western whiptail (*Cnemidophorus tigris*); G.W. = Leopard lizard (*Gambelia wislizenii*); U.s. = Side-blotched lizard (*Uta stansburiana*); P.p. = Desert horned lizard (*Phrynosoma platyrhinos*); S.D. = Western fence lizard (*Sceloporus occidentalis*).

	MONTH					
Habitat	May	June	July	August	September	October
Riparian (a)	0	0	0	1 U.s.	0	0
Riparian (b)	1 C.t.	1 C.t.	1 C.t.	0	0	1 U.s.
Talus (a)	4 U.s. 1 S.o.	2 U.s. 1 C.t.	1 C.t.	0	0	0
Talus (b)	0	4 S.o.	2 U.s.	0	0	1 U.s.
Rim (a)	0	1 S.o.	2 C.t.	0	0	5 U.s.
Rim (b)	0	0	0	1 U.s.		7 U.s.
Shadscale (a)	2 U.s. 2 P.p.	7 C.t. 2 P.p. 3 G.w.	1 C.t.	2 C.t. 1 U.s.	1 U.s.	-
Shadscale (b)	5 U.s.	1 G.w.	0	0	0	15 U.s.
Big Sage (a)	0	6 C.t.	1 C.t.	-	-	-
Big Sage (b)	1 G.w.	3 G.w. 1 C.t.	0	-	-	-
Winterfat (a)	1 U.s.	1 U.s.	0	-	-	-
Winterfat (b)	0	0	0	-	-	-
Lizard Totals	12 U.s. 1 C.t. 1 S.o. 2 P.p. 1 G.w.	3 U.s. 16 C.t. 5 S.o. 2 P.p. 7 G.w.	2 U.s. 6 C.t.	3 U.s. 2 C.t.	1 U.s.	29 U.s.
Month Totals	17	33	8	5	1	*29

*Many of this total represent young of the year.

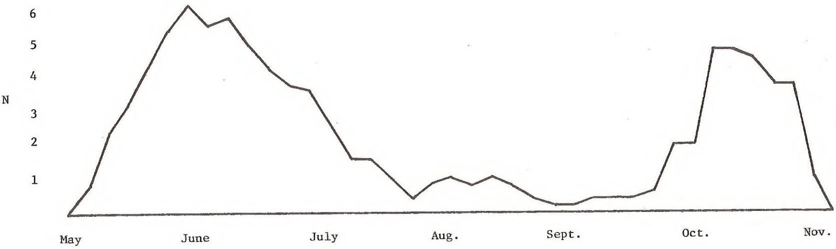
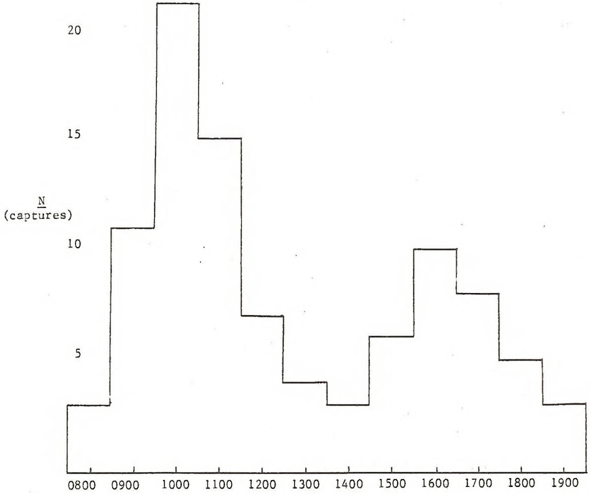


Fig. 2. Histogram of 1978 lizard drift fence captures. (25 day moving average)



Time of day

Fig. 3. Daily activity pattern of the short-horned lizard (Phrynosoma douglassi) in Central Oregon (Diller 1973 - unpublished data).

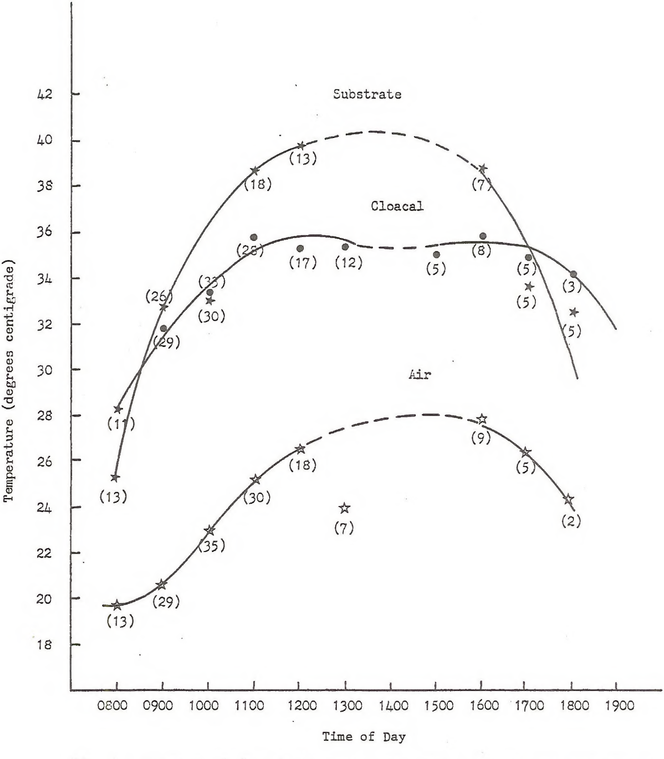


Fig. 4. Substrate, body and air temperature curves derived from short-horned lizards (Phrynosoma platyrhinos) at time of capture in central Oregon (Diller 1973 - unpublished data).

thermoregulation, which mainly involves moving in and out of sunlight. Bimodal activity patterns typically result when midday heat makes it difficult for a lizard to maintain its preferred body temperature. The preferred body temperatures for lizards in the BPSA range from 35 to 40° C and these temperatures are best maintained when air temperatures range from 20 to 30° C (Brattstrom 1965; Heath 1965; Tanner and Krogh 1973 and 1974; Pianka and Parker 1975; Parker and Pianka 1976; Schall 1977).

Snake Density and Biomass

Table 5 summarizes all recorded captures of snakes in the BPSA. Some of the captures resulted from fortuitous encounters by various personnel of the Birds of Prey research project, but most of the captures were made by members of this study. No attempt has been made to remove biases resulting from unequal time spent in different habitat types, or detectibility of the different species of snakes. Thus, these data cannot be used to calculate relative density estimates, but they do reveal certain trends. Gopher and rattlesnakes appear to be about equally likely to be encountered in the BPSA, followed by the striped whipsnake (*Masticophis taeniatus*). All other snake species were encountered too infrequently to speculate on their abundance. These data also indicate that rocky areas like the canyon rim and rocky outcrops probably have the highest density of snakes.

Snake density estimates in the various cover types/habitats were calculated from drift fence captures (see Methods). These data are summarized in Table 6. Gopher snakes (N = 100) were the most frequently captured in drift fences, followed closely by striped whipsnakes (N = 81). All other snake species were captured far less frequently, with captures of 32 night snakes (*Hypsiglena torquata*), 24 long-nosed snakes (*Rhinocheilus lecontei*), 14 western rattlesnakes, 12 racers (*Coluber constructor*) and 6 western ground snakes (*Sonora semiannulata*). No western terrestrial garter snakes (*Thamnophis elegans*) were captured in the drift fences. When drift fence captures are converted to density estimates and species specific movement rates were compensated for, certain snake species, especially the night snake and western ground snake, appeared to be more abundant than would otherwise be expected. It is of interest to note that night snakes appear to be least abundant in the BPSA based on hand captures (Table 5), but have one of the higher density estimates based on drift fence captures.

Table 5. Number of snakes hand captured in various cover types/habitats. C.v. = western rattlesnake (Crotalus viridis); P.m. = gopher snake (Pituophis melanoleucus); M.t. = striped whipsnake (Masticophis taeniatus); S.s. = western ground snake (Sonora semiannulata); R.l. = long-nosed snake (Rhinocheilus lecontei); C.c. = racer (Coluber constrictor); T.e. = western terrestrial garter snake (Thamnophis elegans); H.t. = night snake (Hypsiglena torquata).

		Snake Species								
Cover type/Habitat		C.v.	P.m.	M.t.	S.s.	R.l.	C.c.	T.e.	H.t.	Habitat Totals
Big Sage	N	22	46	4	1	2	0	0	0	75
	%	6.6	14.3	2.4	4.0	22.2	0	0	0	8.6
Winterfat	N	6	25	13	0	0	0	0	0	44
	%	1.8	7.8	7.8	0	0	0	0	0	5.1
Shadscale	N	8	12	15	0	2	0	0	0	37
	%	2.4	3.7	9.0	0	22.2	0	0	0	4.3
Greasewood	N	3	14	1	0	2	0	0	0	20
	%	0.9	4.3	0.6	0	22.2	0	0	0	2.3
Grass	N	9	30	7	8*	0	0	0	0	54
	%	2.7	9.3	4.2	32.0	0	0	0	0	6.2
Canyon rim	N	160	25	43	0	1	0	0	0	229
	%	47.9	7.8	25.9	0	11.1	0	0	0	26.3
Rocky outcrop	N	102	27	39	2	0	0	0	2	172
	%	30.5	8.4	23.5	8.0	0	0	0	66.7	19.8
Talus	N	7	23	25	9	0	0	0	1	65
	%	2.1	7.1	15.1	36.0	0	0	0	33.3	7.5
Riparian	N	13	58	19	3*	0	3	4	0	100
	%	3.9	18.0	11.4	12.0	0	50.0	80.0	0	11.5
Sandy	N	1	0	0	2	0	0	0	0	3
	%	0.3	0	0	8.0	0	0	0	0	0.3
Agricultural lands	N	3	62	0	0	2	3	1	0	71
	%	0.9	19.3	0	0	22.2	50.0	20.0	0	8.2
Snake totals		334	322	166	25	9	6	5	3	870

*All of these captures were made near the base of talus slopes.

Rattlesnakes were the only snakes recaptured frequently enough to estimate their density by mark-recapture methods. After repeated searches in an area, we reached a point where all rattlesnakes captured were previously marked, and thus total number marked represents a minimum population estimate (Tinkle 1967). In this manner density estimates of 6.6, 5.6 and 4.5 snakes per hectare, and biomass estimates of 2639, 2239, and 1799 g/ha were obtained for Trio Butte, the north rim of "Tom Draw" and the east rim of "Tick City Basin", respectively (see Fig. 1 for locations).

A removal census of rattlesnakes in 1976 along the rim between "Dedication Point" and "Dedication Site" yielded 27 snakes in 7 successive searches over a 9-day period for a density estimate of 11.0 snakes per hectare and biomass estimate of 4398 g/ha. During the remainder of that field season, 8 additional snakes were found in this area, but were not included in the density estimate because of possible immigration into the area. During the 1977 field season, only 3 additional rattlesnakes were found in the censused area indicating that the snakes had been effectively removed the previous summer.

Drift fence captures (Table 6) also support the conclusion made above that rocky habitats had the highest density of snakes. Density estimates from canyon rim and talus habitats were about twice as high as those from most other habitats. (We were unable to set up drift fences to sample rocky outcrops, but we would expect similar densities in these areas as occurred in other rocky areas.) After the two rocky habitat types, greasewood had the highest estimates of snake density and biomass, followed closely by riparian, shadscale and sandy habitats. The lowest estimates were obtained for big sage, grass and winterfat habitats.

The abundance and size of an organism can be considered as one measure of its importance in an ecosystem. Table 7 summarizes the potential importance of each snake species in the BPSA, based on drift fence captures. From this it would appear that gopher snakes and western rattlesnakes are the most important snakes. Gopher snakes are the most ubiquitous and have the second highest mean biomass estimate, while rattlesnakes were captured in only one third of the drift fences, but had by far the highest mean biomass estimates. (It should be noted that western rattlesnakes were observed in all habitats (Table 5), but were not captured in drift fences in some of these habitats. This points out one flaw in the drift fence

Table 6. Snake drift fence census. P.m. = gopher snake (Pituophis melanoleucus); M.t. = striped whipsnake (Masticophis taeniatus); H.t. = night snake (Hypsiglena torquata); R.l. = long-nosed snake (Rhinocheilus lecontei); C.v. = western rattlesnake (Crotalus viridis); C.c. = racer (Coluber constrictor); S.s. = western ground snake (Sonora semiannulata).

Drift fence	Number density biomass	P.m.	M.t.	H.t.	R.l.	C.v.	C.c.	S.s.	D.f. totals	Habitat means
*Canyon rim (a)	n	5(1)	4	2	--	1	--	--	12	
	n/ha	1.51	1.22	2.16		1.08			5.97	
	g/ha	304.56	124.68	31.14		422.71			883.09	
*Canyon rim (b)	n	5	7(1)	5	--	3	--	--	20	
	n/ha	1.51	2.13	5.41		3.23			12.28	
	g/ha	304.56	218.19	77.84		1268.14			1989.12	
Canyon rim (c)	n	8(1)	5	5(1)	--	3	--	--	21	17.67
	n/ha	2.41	1.52	5.41		3.23			12.57	10.27
	g/ha	487.29	155.85	77.84		1268.14			1989.12	1580.31
*Talus (a)	n	8	9(1)	6	--	1	1	3	28	
	n/ha	2.41	2.74	6.49		1.08	0.29	13.64	26.65	
	g/ha	487.29	280.53	93.41		422.71	22.42	107.73	1414.09	
*Talus (b)	n	6(1)	6(1)	3	--	--	--	--	15	
	n/ha	1.81	1.83	3.24					6.88	
	g/ha	365.47	187.02	46.70					599.19	
Talus (c)	n	--	3	1	4(1)	3	--	3	14	19.00
	n/ha		0.91	1.08	1.44	3.23		13.64	20.30	17.94
	g/ha		93.51	15.57	105.56	1268.14		107.73	1590.51	1201.26
*Riparian (a)	n	7(3)	7(3)	--	--	--	5	--	19	
	n/ha	2.11	2.13				1.45		5.69	
	g/ha	426.38	218.19				112.08		756.65	
*Riparian (b)	n	6	5(1)	--	--	--	5	--	16	
	n/ha	1.81	1.52				1.45		4.78	
	g/ha	365.47	155.85				112.08		633.40	
Riparian (c)	n	6	2	--	--	--	--	--	8	14.33
	n/ha	1.81	0.61						2.42	4.30
	g/ha	365.47	62.34						427.81	605.95

Table 6. continued

Drift fence	Number density biomass	P.m.	M.t.	H.t.	R.l.	C.v.	C.c.	S.s.	D.f. totals	Habitat means
Sandy (a)	n	5(1)	4(1)	--	1	1	--	--	11	
	n/ha	1.51	1.22		0.36	1.08			4.17	
	g/ha	304.56	124.68		26.39	422.71			878.34	
Sandy (b)	n	3	--	--	--	--	--	--	3	7.0
	n/ha	0.91							0.91	2.54
	g/ha	182.73							182.73	530.54
Greasewood (a)	n	5	3(1)	--	5	1	--	--	14	
	n/ha	1.51	0.91		1.81	1.08			5.31	
	g/ha	304.56	93.51		131.95	422.71			952.73	
Greasewood (b)	n	6(1)	--	3	1	--	--	--	10	12.00
	n/ha	1.81		3.24	0.36				5.41	5.36
	g/ha	365.47		46.70	26.39				438.56	695.64
*Shadscale (a)	n	3	4(2)	5	3	--	--	--	15	
	n/ha	0.91	1.22	5.41	1.08				8.62	
	g/ha	182.73	124.68	77.84	79.17				464.42	
*Shadscale (b)	n	7(4)	6(1)	2	--	--	--	--	15	
	n/ha	2.11	1.83	2.16					6.10	
	g/ha	426.38	187.02	31.14					644.54	
Shadscale (c)	n	1	2	--	--	--	--	--	3	
	n/ha	0.30	0.61						0.91	
	g/ha	60.91	62.34						123.25	
Shadscale (d)	n	1	3	--	6(1)	1	--	--	11	11.00
	n/ha	0.30	0.91		2.17	1.08			4.46	5.02
	g/ha	60.91	93.51		158.34	422.71			735.47	491.92
*Big sage (a)	n	2	4	--	--	--	--	--	6	
	n/ha	0.60	1.22						1.82	
	g/ha	121.82	124.68						246.50	

Table 6. continued

Drift fence	Number density biomass	P.m.	M.t.	H.t.	R.l.	C.v.	C.c.	S.s.	D.f. totals	Habitat means
*Big sage (b)	n	1	—	—	—	—	1	—	2	
	n/ha	0.30					0.29		0.59	
	g/ha	60.91					22.42		83.33	
Big sage (c)	n	9(1)	1	—	2(1)	—	—	—	12	
	n/ha	2.72	0.30		0.72				3.74	
	g/ha	548.20	31.17		52.78				632.15	
Big sage (d)	n	1	4(1)	—	1	—	—	—	6	6.50
	n/ha	0.30	1.22		0.36				1.88	2.50
	g/ha	60.91	124.68		26.39				211.98	293.49
*Winterfat (a)	n	1	—	—	—	—	—	—	1	
	n/ha	0.302							0.302	
	g/ha	60.91							60.91	
*Winterfat (b)	n	—	2	—	—	—	—	—	2	1.5
	n/ha		0.609						0.609	0.46
	g/ha		62.34						62.34	61.62
Grass	n	4	—	—	1	—	—	—	5	5
	n/ha	1.21			0.36				1.57	1.57
	g/ha	243.65			26.39				270.04	270.04
Captive totals		100(13)	81(12)	32(1)	24(3)	14	12	6	269	
Snake means	n	4.17	3.38	1.33	1.00	0.58	0.50	0.25		11.21
	n/ha	1.26	1.03	1.44	0.36	0.63	0.15	1.14		6.01
	g/ha	253.80	105.20	20.76	26.39	246.58	11.21	8.98		672.92

* Drift fences with asterisks were operated in 1978 on the north side of the Snake River - all others were operated in 1979 on the south side of the river.

**Numbers in parentheses represent recaptures - they are not included as drift fence captures.

Table 7. Relative importance of snake species in the BPSA.

Snake species	Percent Occurrence in drift fences	*Mean density(n/ha)	*Mean biomass(g/ha)
Gopher snake	91.7	1.37(±0.778)	276.87(±156.97)
Striped whipsnake	79.2	1.30(±0.624)	132.88(±63.92)
Western rattlesnake	33.3	1.89(±1.113)	739.68(±437.61)
Night snake	37.5	3.84(±1.884)	55.35(±27.089)
Long-nosed snake	37.5	0.96(±0.701)	70.37(±51.104)
Racer	16.7	0.87(±0.670)	67.25(±51.765)
Ground snake	8.3	13.64	107.73

*Mean values represent averages from the drift fences where the snake species was captured.

density estimates. The density of snakes in a particular habitat has to be above some minimum level before any drift fence captures will occur.) Striped whipsnakes probably rank third in importance, since they are widespread and rank beneath gopher snakes in mean biomass estimates. The remaining snake species are all of lesser importance, and it would be futile to attempt to rank them.

Snake Habitat Preference

Habitat preference of different snake species in the BPSA is indicated by the locations where snakes were observed (Table 5) and drift fence density estimates (Table 8). Western rattlesnakes, night snakes and to a lesser extent striped whipsnakes all show an affinity for rocky areas. Rattlesnakes are found most often in rocky outcrops and on the canyon rim, and to a lesser extent in talus slopes. Whipsnakes and night snakes appear to be most abundant in all three of the above mentioned rocky habitats, but whipsnakes also frequent a variety of other habitats. Racers and western terrestrial garter snakes are quite restricted in habitats, and occur in the more moist areas associated with riparian habitats and agricultural lands. The snake with the most restricted habitat preference is probably the western ground snake, which seems almost always to be associated with a talus or scree slope. Gopher snakes and long-nosed snakes appear not to exhibit any obvious habitat preference, with the gopher snake being particularly ubiquitous. One interesting note concerning the long-nosed snake is that it is far more abundant on the south side of the Snake River in the BPSA, than on the north side of the river.

Snake seasonal and daily activity patterns

Frequency of snake captures in drift fences directly reflects seasonal snake activity. Table 9 and Fig. 5 summarize the frequency of snake captures from May to October in 1978. The months of greatest activity are again May and June, as was seen for lizards. However, in contrast to lizards, the actual peak of snake activity occurs during the last two weeks of May, and there is no secondary peak in the fall. From the peak of activity in late May, activity drops off sharply in June and remains at a fairly constant low level throughout the rest of the summer and early fall. By the end of October most snakes are in hibernation, and activity has ceased. The initiation of activity in the spring is not accurately represented in Fig. 5,

Table 8. Habitat preference of snakes as indicated by drift fence density estimates.

Cover type/ habitat	Gopher Snake	Striped Whipsnake	Night Snake	Long-nosed Snake	Western Rattlesnake	Racer	Ground Snake	Habitat means
Big sage	0.98	0.91	---	0.27	---	0.07	---	0.32
Winterfat	0.51	0.30	---	---	---	---	---	0.06
Shadscale	1.11	1.14	1.89	0.81	0.27	---	---	0.75
Greasewood	1.66	0.45	1.62	1.08	0.54	---	---	0.76
Grass	1.21	---	---	0.36	---	---	---	0.22
Canyon rim	1.81	1.62	4.33	---	2.51	---	---	1.47
Talus	1.41	1.83	3.60	0.48	1.44	0.10	9.08	2.56
Riparian	1.91	1.42	---	---	---	0.97	---	0.61
Sandy	1.21	0.61	---	0.18	0.54	---	---	0.36
Snake means	1.27	0.99	1.27	0.35	0.59	0.13	1.01	

Table 9. Seasonal snake activity as represented by monthly drift fence captures in 1978. M.t. = Striped whipsnake (*Masticophis taeniatus*); P.m. = Gopher snake (*Pituophis melanoleucus*); H.t. = Night snake (*Hypsiglena torquata*); C.c. = Racer (*Coluber constrictor*); C.v. = Western rattlesnake (*Crotalus viridis*); S.s. = Western ground snake (*Sonora semiannulata*); R.l. = Long-nosed snake (*Rhinocheilus lecontei*).

Habitat (grid coordinates)	May	June	July	August	September	October
*Riparian (a)	6(2) P.m. 7(1) M.t. 5 C.c.	1 P.m. (1)M.t.	3(1) P.m. 3 M.t.	1 M.t.	0	1 P.m.
*Riparian (b)	2 P.m. 3 M.t.	4 P.m. 2 M.t. 4 C.c.	1 M.t. 1 C.c.	1 H.t. 1 C.c.	2 M.t.	2 C.c.
*Talus (a)	5 P.m. 6 M.t. 1 C.c. 3 H.t.	3 P.m. 2 M.t. 3 H.t. 2 S.s. 1 C.v.	2(1) M.t. 1 S.s.	1 P.m. 3 M.t.	1 P.m. 3 M.t.	0
*Talus (b)	3 P.m. 7(1) M.t. 1 H.t.	4 P.m. 1 H.t.	1 H.t.	1 P.m. 4 M.t.	2 P.m. 1 M.t. 1 H.t. 1 S.s.	1 P.m.
*Rim (a)	3 P.m. 2 M.t.	3(1) P.m. 1 M.t. 1 C.v. 1 H.t.	1 M.t.	1 P.m. 1 M.t. 5 C.v.	3 M.t.	2 M.t.
Rim (b)	3 P.m. 4 M.t. 3 H.t.	2 P.m. 3(1) M.t. 2 C.v. 4 H.t.	1 P.m. 1 M.t. 2 H.t. 1 C.v.	0	1 M.t. 1 H.t.	1 M.t.
*Shadscale (a)	2 P.m. 5(2) M.t. 2 H.t. 1 R.l.	1 P.m. 1 M.t. 2 H.t. 1 R.l.	1 M.t. 1 H.t. 2 R.l.	1 R.l.	1 R.l. 2 M.t.	1 M.t.
Shadscale (b)	8(2) P.m. 5 M.t. 1 H.t.	1 P.m. 1 M.t.	2(1) P.m. 1 M.t. 1 H.t.	1 M.t.	3 M.t.	1 P.m.
Big Sage (a)	1 P.m. 4 M.t.	1 P.m.	0	--	--	--
*Big Sage (b)	0	1 P.m.	1 C.c.	--	--	--
Winterfat (a)	0	0	1 P.m.	--	--	--
*Winterfat (b)	1 M.t.	0	1 M.t.	--	--	--
Snake Totals	33(4) P.m. 44(4) M.t. 10 H.t. 6 C.c. 1 R.l.	21(1) P.m. 11(2) M.t. 11 H.t. 4 C.c. 4 C.v. 1 R.l. 2 S.s.	7(2) P.m. 11(1) M.t. 5 H.t. 2 C.c. 1 C.v. 2 R.l. 1 S.s.	3 P.m. 10 M.t. 1 H.t. 1 C.c. 5 C.v. 1 R.l.	3 P.m. 15 M.t. 2 H.t. 1 R.l. 1 S.s.	3 P.m. 4 M.t. 2 C.c.
Month Totals	94	54	28	21	22	9

NOTE: Numbers in parentheses represent number of total recaptures.
*Drift fences were in operation 8 days during April with only one gopher snake caught.

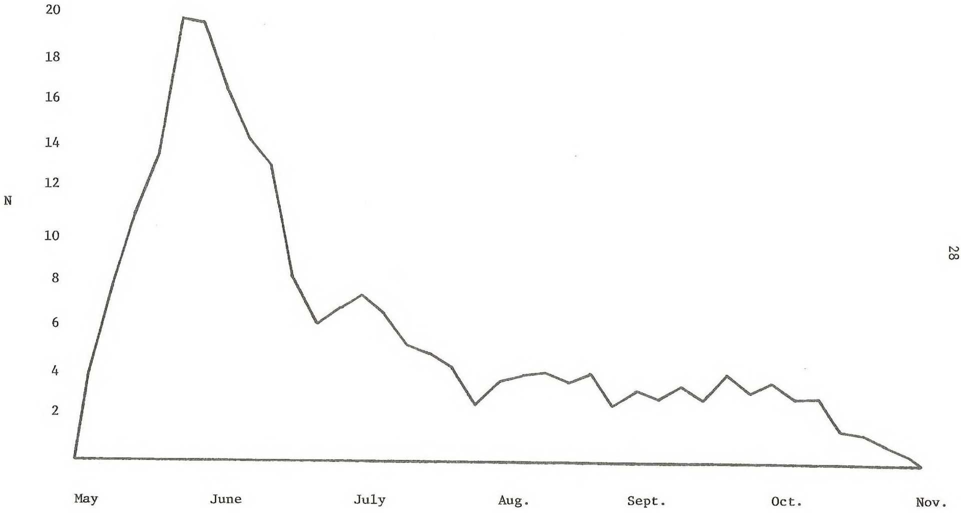


Fig. 5. Histogram of 1978 drift fence captures for all snakes combined (25 day moving average)

since the drift fences were not in operation until the end of April. However, I would not expect many captures, even if the drift fences had been in operation earlier. Snakes can be found out sunning near their hibernaculum (den site) in late March and April, but they do not begin to disperse and thus are not susceptible to trapping until later in the spring.

Most snake species in the BPSA appear to have quite similar seasonal activity patterns. The plots of all capture dates for western rattlesnakes, gopher snakes and striped whipsnakes (Fig. 6, 7 and 8, respectively) are very similar, with a possible exception that striped whipsnakes show a small secondary peak of activity in the fall, while the other two species do not. Western rattlesnakes may also have a somewhat different aspect to their seasonal activity which does not show in Fig. 6. Drift fence captures as seen in Table 9 closely follow total capures (Figs. 6, 7 and 8) for gopher snakes and striped whipsnakes, but not for western rattlesnakes. Rattlesnakes were not readily capured in drift fences, but the captures that did occur were mostly in June, July and August with no sharp peak in May. Apparently rattlesnakes are active near the hibernacula in the spring and susceptible to hand capture, but do not disperse and move about sufficiently to be susceptible to drift fence captures until the summer months. In contrast, gopher snakes and striped whipsnakes must disperse away from the hibernacula, with little delay, after emerging in the spring.

The remaining snake species in the BPSA were not captured in sufficient numbers to make plots of their seasonal activity. However, some speculations can be made from the available data. Racers and longnose snakes seem to have the same general activity pattern that was seen for gopher snakes and striped whipsnakes. Night snakes do not appear to have a sharp peak of activity in May, but instead are about equally active throughout May and June, with activity gradually dropping off during the rest of the summer. Cold nights in the spring probably suppress their activity, since they are nocturnal. Ground snakes were mostly captured in June, July and August and appear to have the most delayed activity period of any snake in the BPSA. Not enough is known about this snake species to speculate on the reason for this.

Figs. 6, 7 and 8 also indicate that there are some differences between the sexes in seasonal activity. Females do not show as sharp a peak of activity in the spring, and their peak of activity is later than males for

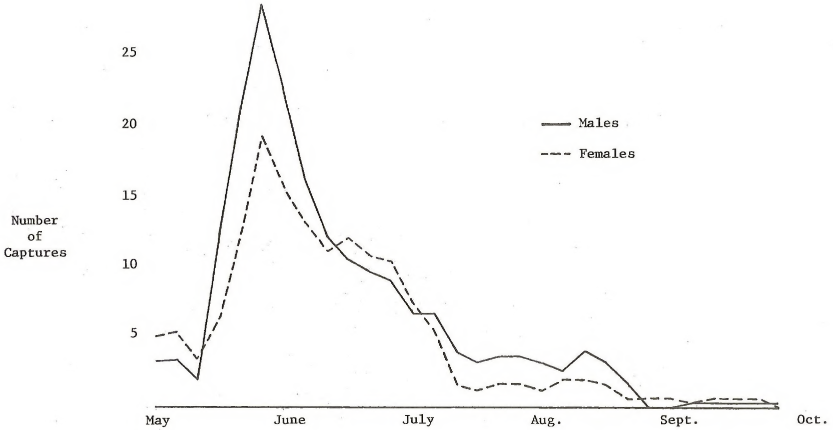


Fig. 6. Seasonal activity of male and female western rattlesnakes as indicated by frequency of captures. (15 day moving average)

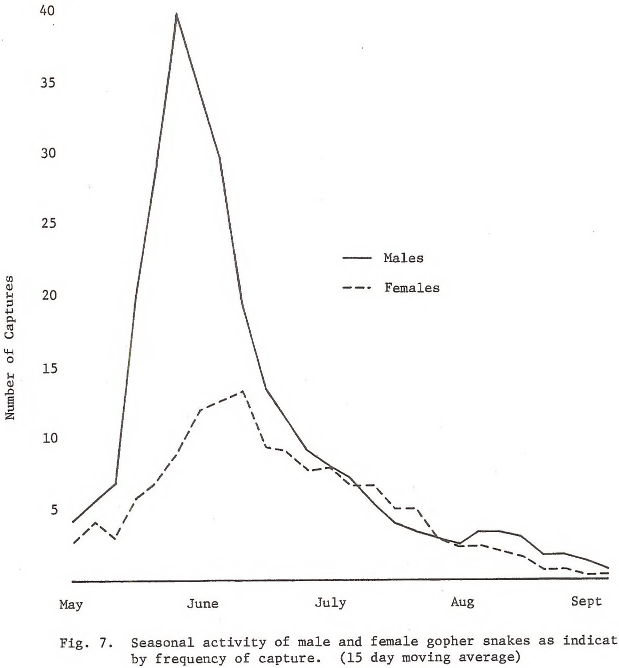


Fig. 7. Seasonal activity of male and female gopher snakes as indicated by frequency of capture. (15 day moving average)

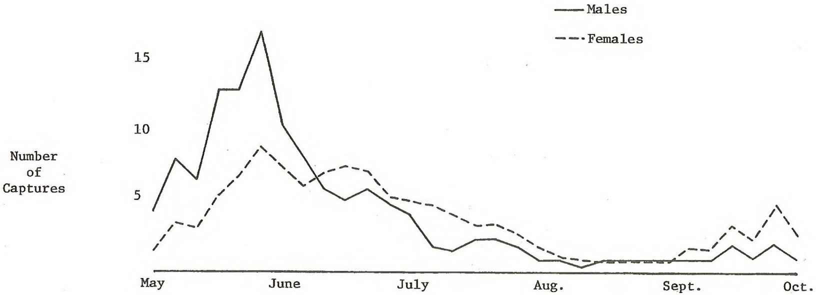


Fig. 8. Seasonal activity of male and female striped whipsnakes as indicated by frequency of captures. (15 day moving average)

both gopher snakes and striped whipsnakes. This early sharp peak of activity for males is probably necessary to ensure that they will be ready for breeding when the females emerge (Parker 1974). Western rattlesnakes do not show this difference in activity between the sexes. We do not know why western rattlesnakes are different from the other two snake species in this matter.

Daily activity as indicated by histograms of the number of captures at different times of the day is shown in Figs. 9, 10 and 11 for western rattlesnakes, gopher snakes and striped whipsnakes, respectively. All three snake species are similar in being basically diurnal, but some differences do occur. Western rattlesnakes are most active from 1000 until 1300 hours in both spring and summer, with 54% and 62% respectively of all captures occurring during these times (Fig. 9). However, in summer there is a slight secondary peak of activity in the evening, which does not occur in the spring. It is of interest to note that only two captures or observations of rattlesnakes were ever made after dark during the entire study, even though different researchers on the BPSA were often in the field after dark. Unlike western rattlesnakes, gopher snakes change their daily activity pattern dramatically between spring and summer (Fig. 10). In spring it is basically unimodal and similar to the rattlesnakes, while in summer it is strongly bimodal with one peak at midmorning and the other in the evening around dusk. The daily activity pattern for striped whipsnakes (Fig. 11) is quite similar to rattlesnakes and gopher snakes in the spring, with the peak of activity at midday. In summer, their activity pattern remains basically unimodal, except the peak of activity shifts to late morning.

Not enough captures were recorded for the remaining snake species on the BPSA to construct any activity graphs, but some observations can be made about western ground snakes, long-nosed snakes and night snakes. Western ground snakes are considered to be nocturnal by Stebbins (1966). However, in the BPSA they were collected most frequently in daylight hours, with 13 out of 15 captures occurring between 1800 and 2200 hours. Thus in southern Idaho, it would appear that the western ground snake is mainly active around dusk, with some nocturnal activity. Long-nosed snakes are considered to be crepuscular or nocturnal (Stebbins 1966), and our limited observations would tend to indicate that they are crepuscular in southern Idaho. Night snakes were never found active in the daytime, which confirms that they are nocturnal.

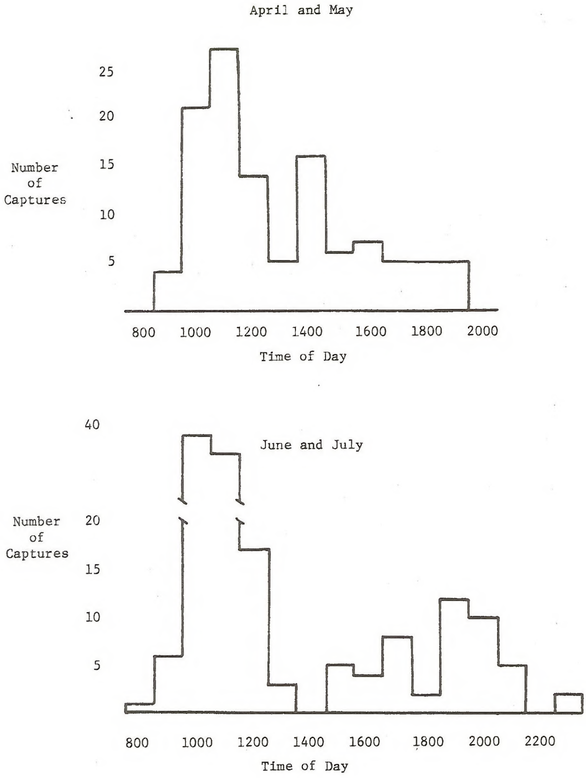


Fig. 9. Daily activity of western rattlesnakes as represented by accumulative times of capture from 1975 to 1979.

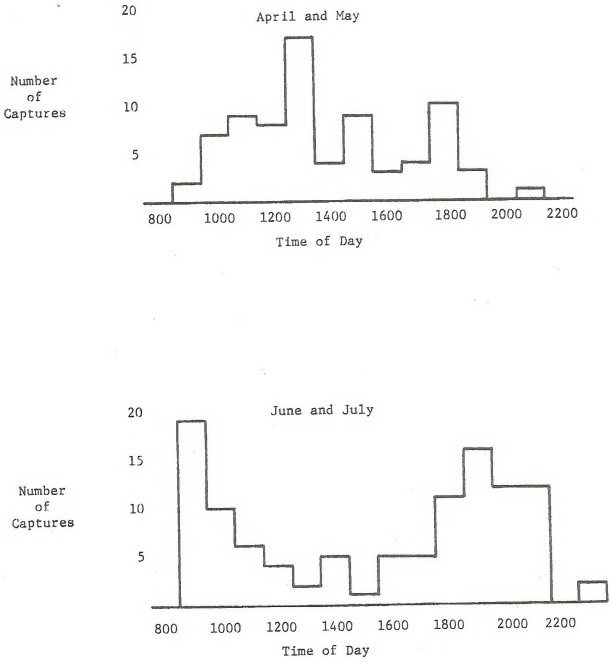


Fig. 10. Daily activity of gopher snakes as represented by accumulative times of capture from 1975 to 1979.

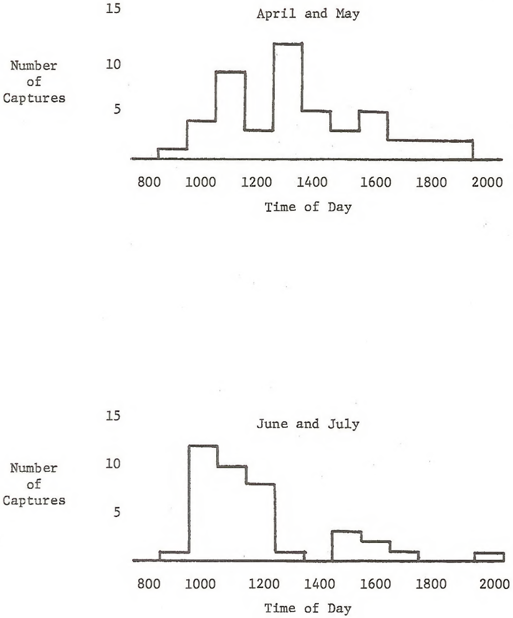


Fig. 11. Daily activity of striped whipsnakes as represented by accumulative times of capture from 1975 to 1979.

Thermal ecology of snakes

Snake activity is influenced strongly by the need to thermoregulate within certain temperature limits. Thus differences in snake activity patterns may result in different thermal strategies. In spite of some differences in activity patterns between western rattlesnakes, gopher snakes and whipsnakes, there appears to be little difference in their thermal regimes as indicated by body, air and substrate temperatures, and weather conditions at time of capture (Table 10 and 11, and Figs. 12, 13 and 14). All three snake species were most frequently captured on a clear sunny day with the air temperature about 22° C, substrate temperature 33° C and snake body temperature of about 30° C.

Probably the only biologically meaningful thermal difference indicated by our data is shown by comparing body and air temperature frequency curves for rattlesnakes and gopher snakes (Figs. 12 and 13). The gopher snake curves do not have peaks as sharp as do the rattlesnake curves, indicating that gopher snakes have a broader range of preferred temperatures. The whipsnake curves are based on insufficient data to allow comparison.

Gopher snakes appeared to show differences in weather conditions preferred for activity as compared to rattlesnakes and whipsnakes. More than 30% of all gopher snake captures occurred when there was some degree of overcast, while about 20% of rattlesnake and whipsnake captures occurred during these types of weather conditions. Considering the scarcity of overcast weather in the BPSA during the summer months, it would appear that gopher snakes are more active during overcast weather than clear weather.

Few temperature data were collected for the other snake species in the BPSA, so that we cannot give their thermal preferences. However, Brattstrom (1965) indicates that snakes which are active during colder seasons or colder times of day usually have lower thermal preferences. Thus, the more nocturnal and aquatic species of snakes in the BPSA, probably have lower thermal preferences than the three diurnal species discussed above.

Movements and home ranges of snakes

Some insights into snake movements and home ranges were provided by the mark-recapture technique. The mean distance travelled between 111 successive captures of western rattlesnakes was 85 m (S.D. = 177.1). How-

Table 10. Body (cloacal), air and substrate temperatures taken at time of capture for western rattlesnakes, gopher snakes and striped whipsnakes.

Temperature °C		Snake Species		
		Western rattlesnake	Gopher snake	Striped whipsnake
Body (cloacal):	N	100	65	26
	mean	27.9 (SD=4.01)	28.6 (SD=4.50)	27.8 (SD=4.27)
	minimum	15.0	17.6	20.0
	maximum	37.0	36.0	33.8
	*preferred	29.8 (SD=3.78)	29.6(SD=3.75)	29.7 (SD=4.25)
Air:	N	220	146	67
	mean	21.8 (SD=3.97)	22.5 (SD=5.30)	21.4 (SD=5.01)
	minimum	13.0	10.8	13.0
	maximum	35.0	38.0	35.0
Substrate:	N	85	43	23
	mean	33.0 (SD=6.12)	33.3 (SD=7.06)	32.6 (SD=4.66)
	minimum	22.0	16.2	25.0
	maximum	50.0	47.0	43.0

*Excludes all captures where conditions would not allow a snake to thermoregulate within its normal range.

Table 11. Summary of weather conditions at time of capture for western rattlesnakes, gopher snakes and striped whipsnakes.

Weather conditions	Western rattlesnake		Gopher snake		Striped whipsnake	
	N	%	N	%	N	%
Clear and sunny	186	80.1	114	68.7	66	82.5
Partial overcast	25	10.8	25	15.1	4	5.0
Overcast	19	8.2	22	13.2	9	11.2
Heavy overcast - rain	5	0.9	5	3.0	1	1.2

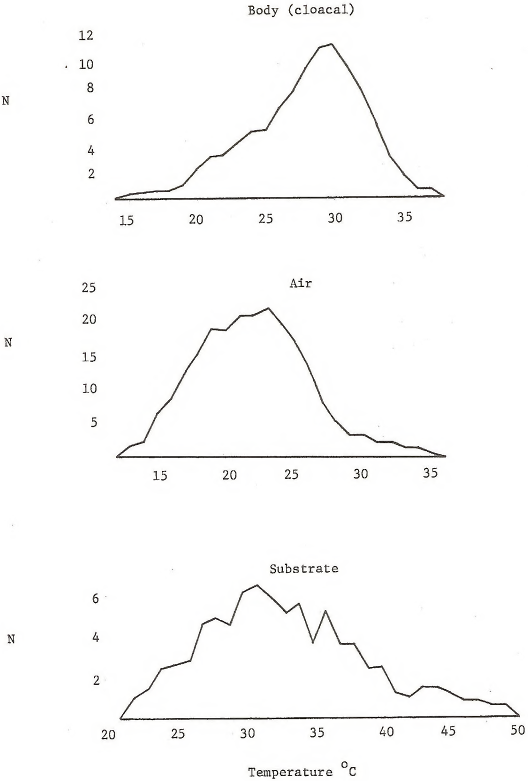


Fig. 12. Frequency of body (cloacal), air and substrate temperatures at time of capture for western rattlesnakes. (5°C moving average used to smooth curve)

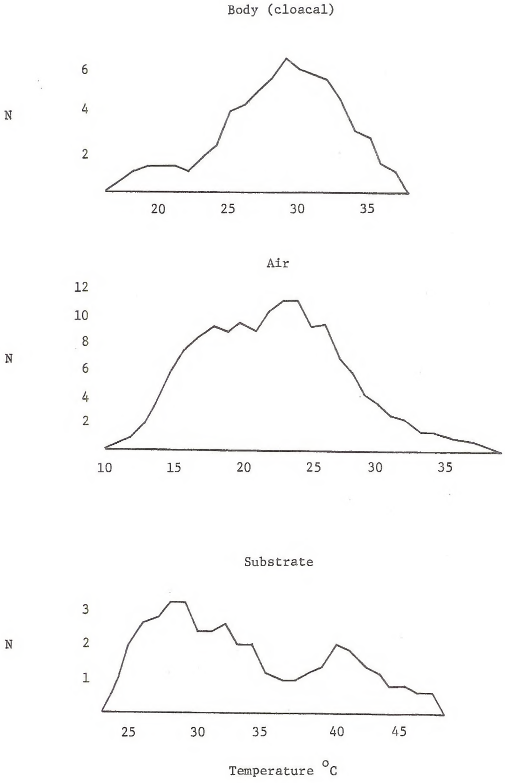


Fig. 13. Frequency of body (cloacal), air and substrate temperatures at time of capture for gopher snakes. (5°C moving average used to smooth curve)

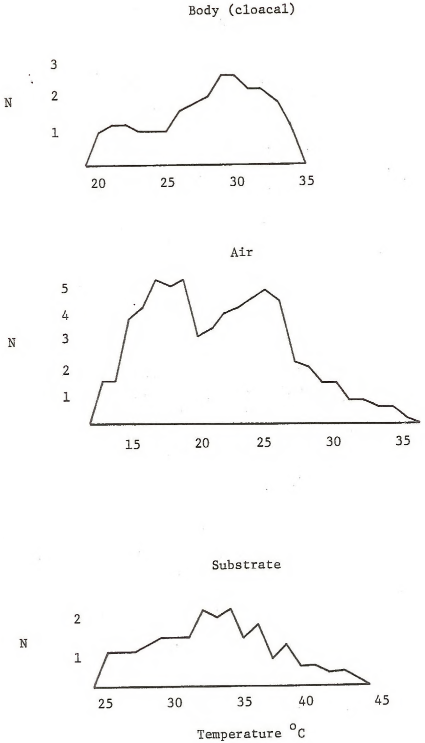


Fig. 14. Frequency of body (cloacal), air and substrate temperatures at time of capture for striped whipsnakes. (5°C moving average used to smooth curve)

ever, rattlesnake movements are better illustrated by the frequency of various recapture distances (Fig. 15), and the relationship of distance travelled to time interval between successive captures (Fig. 16). Over 40% of all recaptures were made at the original capture point with less than 5 m movement. Of the rattlesnakes that made a significant move (> 5 m) between successive captures, 70% travelled between 30 and 150 m with only 16% travelling more than 150 m. It would appear from Fig. 15 that rattlesnakes inhabiting open areas tended to make greater movements. However, this may be due to a collecting bias, which results from searches in rocky outcrops being more restricted than those in open continuous habitat types. Fig. 16 indicates that the distance travelled is poorly correlated to the time interval between successive captures.

Although 190 gopher snakes and 167 striped whipsnakes were marked, only 9 gopher snakes and 7 whipsnakes were ever recaptured where movement could be measured. Tables 12 and 13 record all such movements for gopher snakes and striped whipsnakes, respectively. These recorded movements are too few to describe movement patterns for these two snake species, but these data do suggest that both gopher snakes and striped whipsnakes travel greater distances than do western rattlesnakes. Movements were not recorded for any other snake species in the BPSA.

No individual gopher snake or striped whipsnake was recaptured frequently enough to attempt to estimate home range size, and we feel these species may not have a home range in the traditional sense. However, there is some evidence that western rattlesnakes in the BPSA do exhibit a home range.

An animal that wanders at random would show a strong positive correlation between time interval and distance travelled at successive captures, while an animal with a discrete home range would show no such strong positive correlation between time and distance travelled (Stickel and Cope 1947). Time interval in days was regressed against distance travelled (m) for 79 western rattlesnake recaptures and the regression was not significant (see Fig. 16), indicating that western rattlesnakes meet the criterion for an animal with a home range.

However, of 159 marked rattlesnakes, only 5 were recaptured frequently enough to estimate home range (see Methods). Two adult females had estimated home ranges of 0.8 and 1.0 ha, while three males had estimated home ranges of 0.6, 0.8 and 1.5 ha. Our inability to recapture most individual rattlesnakes frequently enough to estimate their home range may result from the

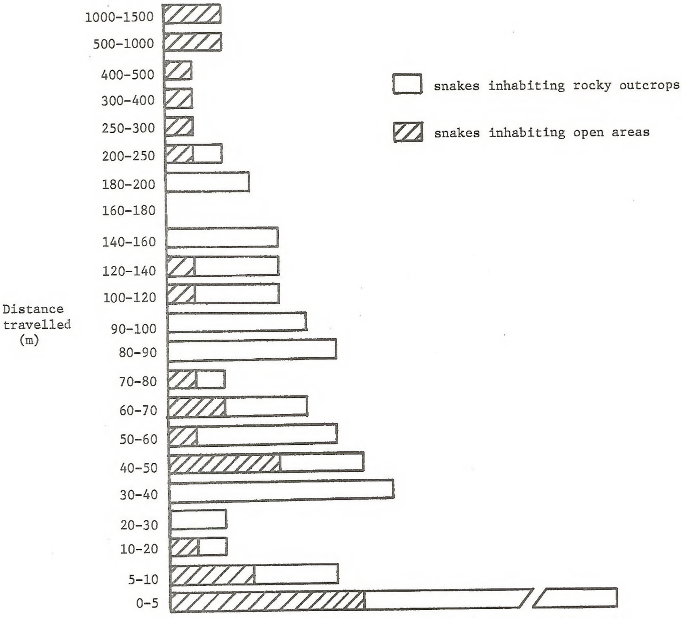


Fig. 15. Movement of western rattlesnakes as indicated by the distance travelled between successive captures.

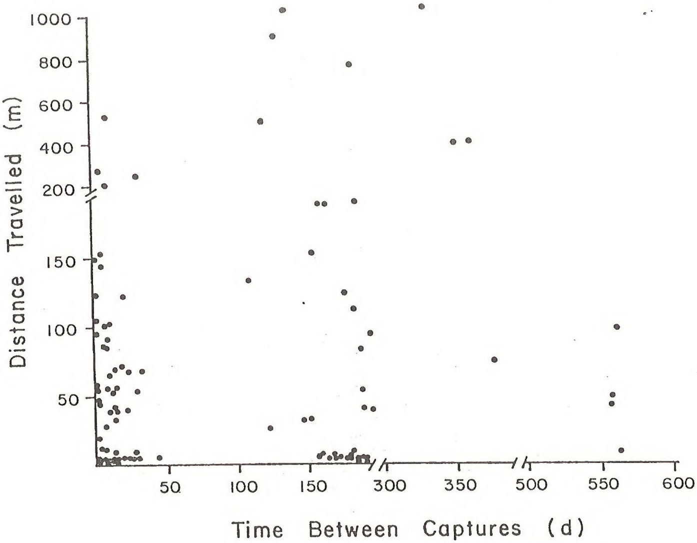


Fig. 16. Relationship of distance travelled to time interval between captures for western rattlesnakes.

Table 12. Movement of gopher snakes

Sex	Snout-vent length (cm)	Capture dates	Distance travelled (m)
Male	105	7-5-75	
		5-19-76	240
		6-25-78	240 (back at original capture site)
Male	109	6-19-75	
		6-25-75	805
Male	113	5-31-77	
		6-15-78	0
Male	88	5-29-77	
		5-29-78	0
Male	93	6-13-77	
		5-24-78	320
Male	92	6-17-77	
		5-17-78	50
Male	97	4-28-78	
		5-4-79	70
Female	107	6-14-76	
		4-29-77	170
Female	74	6-1-78	
		8-10-78	244

n=10
$\bar{x}$=214.3
SD=236.23

Table 13. Movement of striped whipsnakes.

Sex	Snout-vent length (cm)	Capture dates	Distance travelled (m)
Male	112	5-19-77 5-4-78	160
Male	98	5-20-77 5-24-78	360
Male	74	5-21-78 5-4-79	90
Female	87	5-19-77 5-21-78	365
Female	87	6-11-77 6-18-78	100
Female	92	7-3-77 5-11-78	100
Female	87	7-19-77 6-28-78 6-20-79	245 0

$n = 8$
$\bar{x} = 177.8$
$SD = 132.98$

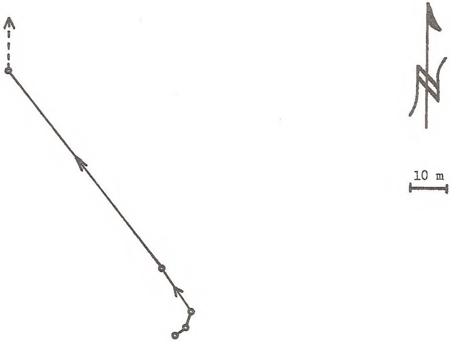
general difficulty of recapturing snakes, or it may indicate that most rattlesnakes do not have home ranges.

The difficulty in recapturing marked snakes led to the radioactive tagging study. Even though radioactive tags could only be monitored at a maximum distance of 4 m, it was assumed that if snakes in the BPSA have home ranges, then repeated searches in the area where the tagged snake was released should eventually produce a recapture of that snake. Although we tagged and released 9 gopher snakes, 7 western rattlesnakes, 3 night snakes, 2 long-nose snakes and 1 striped whipsnake, we were only able to monitor movements of 4 rattlesnakes, 1 gopher snake and 1 night snake with the aid of the radioactive tags. This suggests that snakes that were studied in the BPSA do not have home ranges, with the possible exception of western rattlesnakes. This also seems to be consistent with the mark-recapture study, where rattlesnakes were the only species that was frequently recaptured.

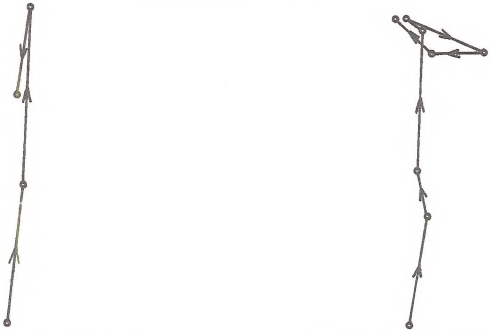
The radioactive tagging study also revealed a possible bias that could indicate why rattlesnakes are more frequently recaptured than other snakes. Whereas rattlesnakes frequently stayed near the surface after being released, most other snakes would enter rodent burrows and travel to depths where it was impossible to detect the radioactive tag.

Although there is some evidence that western rattlesnakes in the BPSA may have home ranges, the movements of three radioactively tagged rattlesnakes that are summarized in Fig. 17 do not suggest the existence of home ranges. These three snakes were the best monitored of any of the tagged snakes, and the movements shown in Fig. 17 occurred during approximately a one month period in each case. (Refer to appendix B for more details on the movements of radioactively tagged snakes.) Their movements suggest that rattlesnakes wander over large areas with no center of activity.

The radioactive tagging study also revealed that snakes will remain in the same location for long periods of time without making a significant move. Four tagged western rattlesnakes were found in 11 different locations with a mean of 5.5 days (range: 1-14, SD = 5.16) spent at each location. Only one gopher snake and one night snake were relocated after the initial release, and they spent 14 days and 2 days, respectively, in the same location. Three of the longest stays in one location for western rattlesnakes and the 14 days spent in one location by a gopher snake all involved ecdysis. After ingesting a large prey item a snake would also be expected to become



Crotalis viridis #644 female



Crotalus viridis #620 female

Crotalus viridis #698 male

Fig. 17. Summarized movements of three radioactively tagged western rattlesnakes. Each open dot indicates a location where the snake resided for a period of time (1-14 days).

more sedentary (observed by the author during feeding studies), so that both ecdysis and feeding would strongly influence the frequency of snake movements.

Although the data are insufficient to establish a general pattern of snake movements in the BPSA, the available information can be summarized and a probable explanation made. In a study of snake movements in Utah, Hirth et al. (1969) felt that snakes in that area could best be described as having a "total range" rather than a home range. The "total range" comprised the hibernaculum (den), the routes to and from the hibernaculum, and all the area that a snake travels over while away from the hibernaculum. The hibernaculum that a snake uses and the routes to and from this hibernaculum are probably relatively constant, but a snake's wanderings on its summer range are quite random.

This concept of a "total range" seems to best explain the data we obtained. Western rattlesnakes were frequently recaptured in spring when they are still concentrated near their hibernaculum and their movements are more predictable. During the summer, recaptures were more difficult to obtain, since the snakes are scattered and their movements are more random. Radioactively tagged snakes were captured and tagged while on their summer range, so that their movements appeared to be somewhat random. The home ranges that were calculated for western rattlesnakes probably resulted from a few individuals that remained near their hibernaculum throughout the summer.

Gopher snakes and striped whipsnakes probably also fit this same pattern. However, they are less conspicuous and spend more time either underground or hidden in cover, so that recaptures are less likely, and it is more difficult to assess their movement patterns.

Snakes such as the long-nose, western ground and night snakes, which are not known to congregate in large numbers at communal hibernacula probably have much different movement patterns than those snakes described above. It is more likely that these snakes have home ranges in the more traditional sense. Barbour et al. (1969) and Clark (1970) studied the movements of two species of the small fossorial worm snake (genus *Carphophis*), and found that they have small, discrete home ranges. The three snake species mentioned above are small and tend to be somewhat fossorial, so they also may have discrete home ranges like the worm snake.

Population structure of snakes

Figs. 18, 19 and 20 show length-frequency distributions for western rattlesnakes, gopher snakes and striped whipsnakes, respectively. Although distinct size classes are obscured by highly variable growth rates of individual snakes, there appear to be five identifiable size classes for western rattlesnakes and gopher snakes, and four size classes for striped whipsnakes. The first size class includes snakes that were born or hatched the previous year. Each succeeding size class includes snakes which are one year older, until the final or adult size class is reached. For western rattlesnakes and gopher snakes, adults include individuals which are over four years old, while adult striped whipsnakes are over three years old. The adult size class could include individuals which are as old as 15-20 years (Fitch 1949).

Male western rattlesnakes reach significantly larger sizes than females (Fig. 18 and Table 14). Males apparently grow more rapidly than females, since they are the same size at birth, but males are significantly larger than females by the start of their third year. Male gopher snakes also reach slightly larger sizes than females, but the difference is not significant (Fig. 19 and Table 15). Male and female striped whipsnakes appear to reach identical sizes, so that they were lumped together in Fig. 20 and Table 16.

It is interesting to note that with one exception, there were more snakes found in each successive age class for all three species of snakes (Tables 14, 15 and 16). It is expected that the adult age class would be the largest in long-lived species, since it includes many year classes. However, if the population is stable, the one year old age group should be the largest single cohort, with a decrease in each successive age class due to mortality. The probable explanation is that there is a bias against collecting smaller snakes, due to their smaller size and/or a difference in their behavior and activity patterns in relation to the larger snakes. This apparent inability to collect all age and size classes equally makes it impossible to construct life tables and calculate mortality rates. However, it is likely from the relative size of the adult age classes, that these snake species have high juvenile mortality and relatively low adult mortality.

Both western rattlesnakes and gopher snakes show an unequal sex ratio, with males being significantly more abundant, when all age classes are

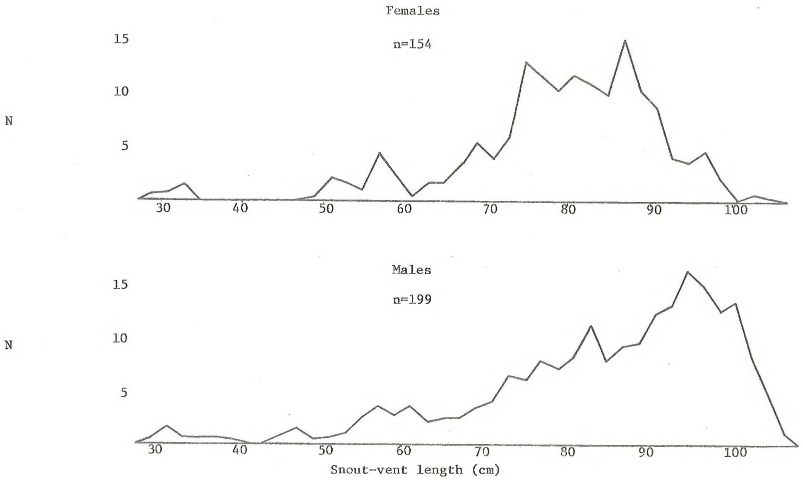


Fig. 18. Length-frequency histogram of western rattlesnakes.

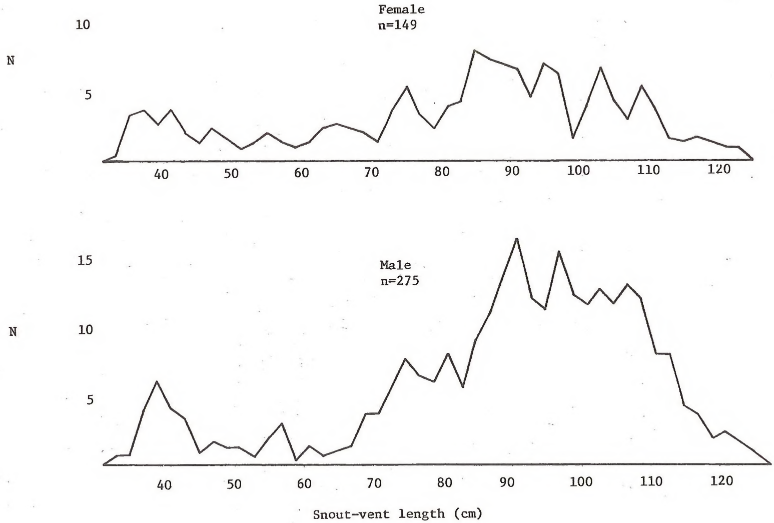


Fig. 19. Length-frequency histogram of gopher snakes.

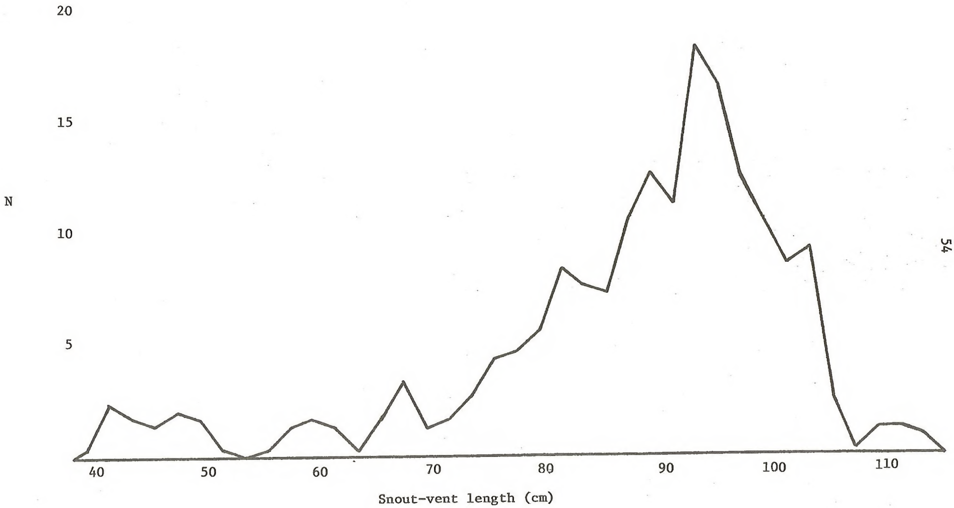


Fig. 20. Length-frequency histogram of striped whipsnakes.

Table 14. Western rattlesnake size classes, age structure and sex ratios.

Snout-vent lengths (mm)

	Males			Females		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD
newborn*	32	277.9	14.9	28	279.5	14.2
1 yr olds	4	329.8	28.7	3	305.7	20.6
2 yr olds	20	577.1	58.9	12	550.4	31.1
3 yr olds	34	738.0	32.5	12	663.2	21.8
4 yr olds	43	839.1	27.6	37	745.8	21.3
>4 yrs old	98	962.7	42.5	90	863.5	54.5
	199			154		

Body weights (g)

	Males			Females		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD
newborn*	32	19.2	3.3	28	18.6	3.3
1 yr olds	4	21.5	5.8	3	14.3	3.5
2 yr olds	20	106.6	32.7	12	84.7	27.1
3 yr olds	34	247.4	63.8	12	169.8	38.0
4 yr olds	42	395.0	81.4	37	295.5	77.0
>4 yrs old	96	591.5	119.5	90	440.1	145.5

*born in captivity

Table 15. Gopher snake size classes, age structure and sex ratios.

Snout-vent lengths (mm)

	Males			Females		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD
newborn*	3	294.7	6.7	6	299.8	10.2
1 yr olds	20	388.4	28.7	16	377.9	28.4
2 yr olds	14	551.6	61.0	12	508.7	43.4
3 yr olds	46	759.3	43.0	25	701.4	53.7
4 yr olds	64	888.4	27.3	44	859.6	37.2
>4 yrs old	131	1045.8	72.4	52	1039.3	78.0
	275			149		

Body weights (g)

	Males			Females		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD
newborn*	3	11.5	0.32	6	11.5	0.9
1 yr olds	18	17.0	3.8	15	14.4	3.4
2 yr olds	11	38.3	14.0	11	34.0	8.1
3 yr olds	46	103.1	21.7	21	87.3	25.4
4 yr olds	61	176.6	34.0	42	170.7	47.4
>4 yrs old	127	304.4	81.4	51	331.1	121.2

*Incubated in captivity from the same clutch

Table 16. Striped whipsnake size classes and age structure.

	Snout-vent lengths (mm)			Body weights (g)		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD
1 yr olds	10	444.0	30.9	10	15.4	2.8
2 yr olds	11	628.3	42.6	11	38.9	6.7
3 yr olds	44	793.7	42.0	43	81.0	23.1
>3 yrs old	116	948.7	55.4	114	135.6	32.4
	181					

combined (Tables 14 and 15). However, the younger age classes do not show a significant difference, indicating that the sex ratio is probably equal at birth. Since males outnumber females in the older age classes, it would appear that females have a higher mortality rate than males. However, there is a possibility that the difference is merely due to males becoming more active and conspicuous with age than their female counterparts, making them more susceptible to capture. It is not shown in Table 16, but striped whipsnakes were captured in an equal sex ratio.

Growth rates of snakes

Natural growth rates of wild snake populations were estimated by three methods. The first method was to measure annual growth in snakes that had been marked and recaptured (Table 17). The next approach was to measure growth in captive snakes and assume that their growth is similar to wild snakes (Table 18). The final method was to calculate mean increases in size between successive age classes (Table 19). Of the three different methods, mark-recapture data tends to yield the lowest estimates of growth rates, with captive snakes having slightly higher growth rates. However, both of these first two methods give much lower estimates of growth than the third method, which was based on age classes.

It is not too surprising that these three different approaches to estimate growth rates would produce different results, since there are problems with each method. To begin with, it is difficult to get enough recaptures of marked snakes to provide good growth data in this manner. Also, I have noted and it has been suggested by Fitch and Glading (1947) that the process of capturing and marking may cause future stunting in the growth of some snakes. This would explain the low growth rates in mark-recapture snakes (Table 17).

Growth rates of captive snakes can be questioned because of the unnatural environment in which they live and feed. Some captive western rattlesnakes and gopher snakes would feed only infrequently or not feed at all. Although these snakes were excluded from calculations of growth, the phenomenon of nonfeeding captive snakes would suggest that there is something about the captive environment that inhibits feeding in at least some snakes. This may indicate that there is a general decrease in appetite in most captive snakes. Decreased appetite would naturally produce reduced growth rates.

Table 17. Growth rates of western rattlesnakes, gopher snakes and striped whipsnakes based on recapture data.

Snake	Snout-vent length (mm/yr)		
	n	$\overline{x}$	SD
Western rattlesnake			
young:	4	57.9	19.0
all others:			
male	16	23.9	14.4
female	16	18.6	10.7
combined	32	21.2	12.8
Gopher snake			
young:	1	114	---
all others:	6	47.3	30.1
Striped whipsnake			
young:	1	93	
all others:	8	35.6	27.4

NOTE: Body weight changes were not included because of small sample sizes and the highly erratic nature of snake weight gain.

Table 18. Growth rates of captive western rattlesnakes and gopher snakes.

Snake	Snout-vent length(mm/d)			Body weight(g/d)		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD
Western rattlesnakes						
young (1 yr olds):						
males	6	0.51(76.5)	0.18	6	0.13(19.5)	0.09
females	7	0.50(75.0)	0.22	7	0.11(16.5)	0.06
combined	13	0.51(76.5)	0.20	13	0.12(18.0)	0.07
all others:						
males	7	0.50(75.0)	0.25	7	0.35(52.5)	0.21
females	5	0.14(21.0)	0.07	5	0.16(24.0)	0.11
combined	12	0.35(52.5)	0.26	12	0.27(40.5)	0.20
Gopher snake						
young (1 yr olds):	11	0.46(69.0)	0.14	10	0.05(7.5)	0.02
2 yr olds:	10	0.63(94.5)	0.28	9	0.15(22.5)	0.08
all others:	17	0.16(24.0)	0.14	9	0.27(40.5)	0.27

*Numbers in parentheses represent estimated yearly growth assuming an average 150 day annual growing season for snakes.

Table 19. Growth rates of western rattlesnakes, gopher snakes and striped whipsnakes based on size and age classes.

Snakes			Snout-vent length (mm/yr)	Body weight (g/yr)
Western rattlesnakes				
	1 yr olds:	males	247.3	85.1
		females	244.7	70.4
	2 yr olds:	males	160.9	140.8
		females	112.8	85.1
	3 yr olds:	males	101.1	147.6
		females	82.6	125.7
Gopher snakes				
	1 yr olds:		147.0	20.4
	2 yr olds:		200.2	59.0
	3 yr olds:		143.6	78.4
Striped whipsnakes				
	1 yr olds:		184.3	23.5
	2 yr olds:		165.4	42.1

Estimating growth from mean increases in the size of successive age classes is also somewhat unreliable, because of the difficulty in accurately determining snake age. This final method is also flawed in that no age classes could be determined after the fourth year, and thus growth rates could only be calculated for the first three years of a snake's life. In spite of the problems with this last method, the estimates of growth rates seen in Table 19 probably best represent natural growth rates for at least younger age classes of snakes, since the first two methods appear to underestimate growth rates.

In spite of these problems, certain observations can be made about growth rates of western rattlesnakes, gopher snakes and striped whipsnakes. Except for the young (1 year olds), male western rattlesnakes have higher growth rates than do females. Male and female gopher snakes and striped whipsnakes had similar growth rates in all age classes, so the sexes were combined in Table 17-19. Also, there is a general trend for all these snakes to increase more rapidly in length when they are young, but increase more rapidly in weight when they are older. However, there was one exception, in that 2 year old gopher snakes appear to increase more rapidly in both length and weight than do 1 year old snakes. I speculate that this results because 2 year old gopher snakes have reached a size where they can take more desirable mammalian prey, whereas the 1 year old snakes are forced to feed on smaller less desirable prey.

Snake reproduction

Annual timing of reproductive events for western rattlesnakes and gopher snakes is given in Figs. 21 and 22, respectively. In both species, mature males were found to have sperm in at least the distal portion of the vas deferens at all times of the year when snakes were collected. However, other studies have shown that the actual spermatogenesis only occurs during the summer months (Goldberg and Parker 1975, and Aldridge 1979). The potential for breeding occurs any time that snakes are active, since mature males always have sperm available and females are able to store sperm (Rahn 1942, and Porter 1972). Breeding activity was seldom observed by us, but the little activity we did see was during the month of May. Apparently most breeding activity occurs in the spring near hibernacula from which snakes have recently emerged, but there are also occasional matings throughout summer and early fall.

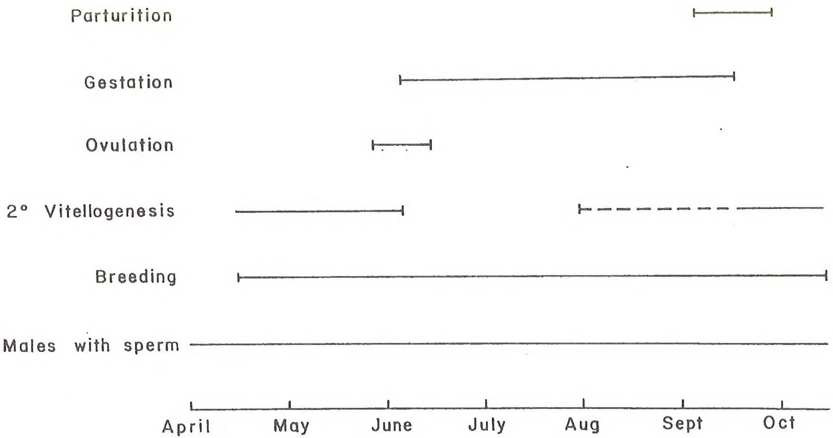


Fig. 21. Reproductive cycle for western rattlesnakes.

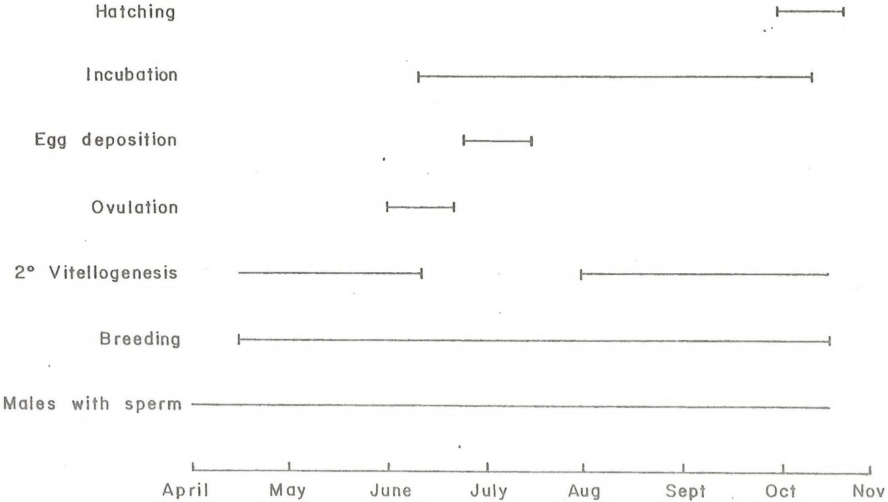


Fig. 22. Reproductive cycle for gopher snakes.

Vitellogenesis is shown as beginning in August for western rattlesnakes (Fig. 21), but this only applies to mature females that are not reproductively active that year, or to females that are just reaching sexual maturity and will reproduce for the first time the next summer. All reproductively active females begin vitellogenesis after parturition in the fall at the earliest.

Ovulation occurs about the same time for both western rattlesnakes and gopher snakes, but young rattlesnakes are born several weeks before gopher snake eggs hatch (Figs. 21 and 22). The reduced developmental time for rattlesnakes results from the embryos being "incubated" in the female's body at higher temperatures than gopher snake eggs experience while being buried in the ground.

The mean clutch size for 33 female western rattlesnakes was 8.3 (range: 5-15, S.D. = 2.4), while 21 gopher snakes had a mean clutch of 6.5 (range: 3-11, S.D. = 2.0). "Reproductive effort" defined (Williams 1966) as the caloric content of a mean clutch of recently ovulated eggs divided by the mean caloric content of a sexually mature female is 0.18 and 0.38 for western rattlesnakes and gopher snakes, respectively. This would indicate that female gopher snakes put a greater caloric "effort" into reproduction. However, if "reproductive effort" is defined as the caloric content of a mean clutch or litter of neonates divided by the mean caloric content of a sexually mature female, then the calculated values are 0.40 and 0.30 for rattlesnakes and gopher snakes, respectively. The decreased value for gopher snakes is expected, since the developing embryos are not totally efficient at converting yolk into body tissue. Therefore this latter calculation of "reproductive effort" does not include the total caloric expenditure per clutch for gopher snakes. The increased value of "reproductive effort" seen for rattlesnakes in the latter calculation indicates that a pregnant female rattlesnake must impart nutrients to the developing embryos during gestation. Thus, this latter calculation of "reproductive effort" in western rattlesnakes is a better estimate of the total caloric "effort" that a female puts into a litter of young.

Comparing the first estimate (0.38) of "reproductive effort" for gopher snakes with the second estimate (0.40) for western rattlesnakes indicates that females in both species expend similar amounts of energy in reproduction. However, virtually all (30 out of 31) sexually mature female gopher snakes reproduce in a given year, while 70% (53 out of 76) of the mature female rattlesnakes reproduce each year. Thus, over a lifetime, female gopher snakes probably invest more into reproduction than do female western rattlesnakes. We had no means to estimate the amount of energy that males of either species invested in reproduction.

There is a positive correlation between clutch size and female size in both western rattlesnakes and gopher snakes (Figs. 23 and 24). The correlation is very good for both species, which indicates that the reproductive potential for larger females is much greater than smaller females. Based on the reproductive condition of dissected snakes, most females from both species reproduce for the first time in their fourth year, with an occasional precocious female reproducing in her third year. At this time they are a minimum of about 70 and 80 cm in snout-vent length for western rattlesnakes and gopher snakes, respectively. Based on the presence of sperm in the vas deferens, male western rattlesnakes reach sexual maturity by the fall of their second year at a minimum snout-vent length of about 56 cm, while male gopher snakes are in the fall of their third year and about 72 cm in snout-vent length when they reach sexual maturity. The delayed sexual maturity of females as compared to males in both species is probably best explained by the greater fecundity that is imparted to larger females as is seen in Figs. 23 and 24.

Few reproductive data were gathered for striped whipsnakes in the BPSA. However, based on Parker (1974), the timing of reproductive events for striped whipsnakes is very similar to gopher snakes. The only breeding activity observed was on 1 May, when three males were seen attempting to copulate with one female. Only three clutches of eggs were recorded for striped whipsnakes and they all contained six eggs. From our limited data, it appears that both male and female whipsnakes reach sexual maturity in three years at a snout-vent length of 70-80 cm. No reproductive data were gathered for any other snake species in the BPSA.

Snake fat body cycles

Fat body size expressed as a percentage of total body weight for male and female western rattlesnakes, gopher snakes and striped whipsnakes is given in Table 20. Seasonal fat body cycles for the same snake species

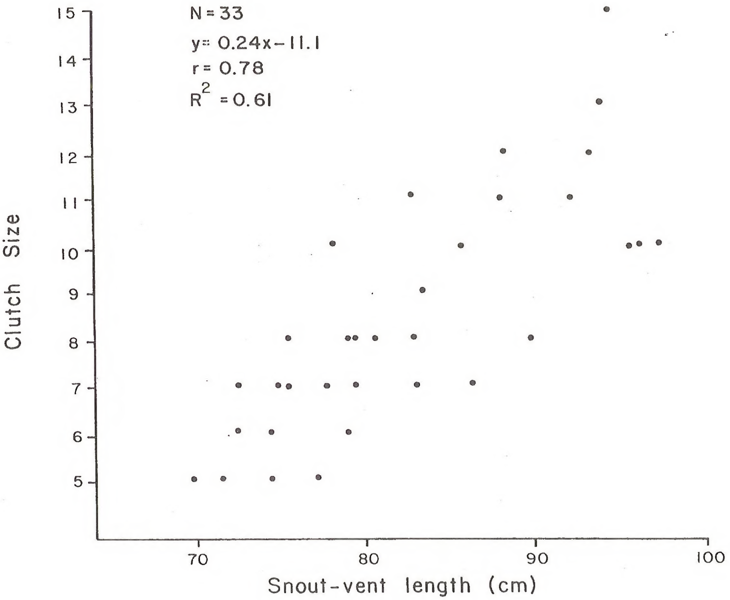


Fig. 23. Regression of clutch size on female size (snout-vent length) for western rattlesnakes.

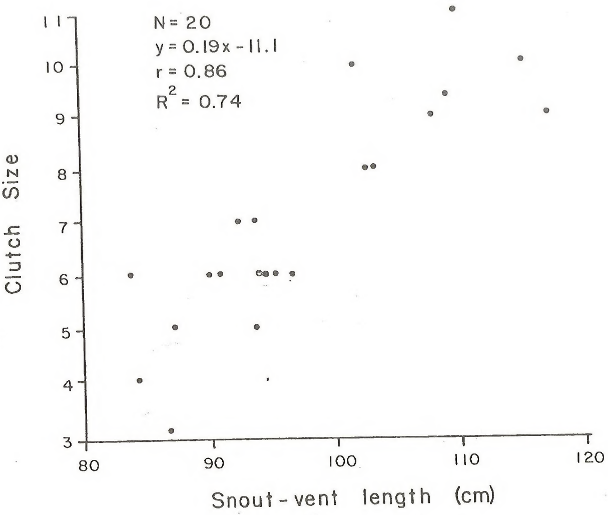


Fig. 24. Regression of clutch size on female size (snout-vent length) for gopher snakes.

Table 20. Fat body size for western rattlesnakes, gopher snakes and striped whipsnakes.

Snake	Fat Body (% body wt.)			
	n	$\bar{x}$	SD	
Western rattlesnake				
males:	61	6.9	4.66	
females:	46	8.4	6.33	t = 1.41
combined:	107	7.6	5.38	
Gopher snake				
males:	51	5.3	3.78	
females:	34	6.7	2.84	t = 1.91
combined:	85	5.9	3.41	
Striped whipsnakes				
males:	20	2.2	1.91	
females	27	4.6	2.49	t = 2.68
combined:	47	3.6	2.25	

are given in Figs. 25-27. Females averaged a greater percent body fat than did males for all three species, but the difference is statistically significant for only striped whipsnakes, because of the high individual variation seen in rattlesnakes and gopher snakes. Western rattlesnakes have the highest percent body fat, followed by gopher snakes and striped whipsnakes.

This high degree of individual variation in fat body size also makes it difficult to identify seasonal cycles, but there appears to be a general decrease in percent body fat over the entire summer for gravid (pregnant) western rattlesnakes, while nonreproductive sexually mature female rattlesnakes show a general increase (Fig. 25). This would be expected if female rattlesnake fat reserves are utilized primarily for reproduction. Reproductive females invest a large amount of energy during vitellogenesis and possibly continue to invest some calories into their developing fetuses during gestation (see Snake reproduction). Also, they typically do not feed during this time (Keenlyne 1972 and data from this study). Nonreproductive females have no such drains on their fat reserves, so their fat stores should increase over summer. As also would be expected, nonreproductive females have a much higher mean percent body fat (n = 17, $\bar{x}$ = 12.7, S.D. = 7.33) than do reproductive females (n - 32, $\bar{x}$ = 6.0, S.D. = 3.66). Most male western rattlesnakes apparently have ample fat reserves, so that no single seasonal event depletes their fat bodies, and a seasonal fat body cycle cannot be identified (Fig. 25).

Female gopher snakes appear to have a bimodal fat body cycle (Fig. 26). Their fat reserves are somewhat depleted when they emerge from hibernation; they build to a peak by early summer, drop to a low point in midsummer corresponding to egg-laying and then increase again during late summer and early fall. There is no separate fat body cycle for nonreproductive sexually mature female gopher snakes, since virtually all mature females reproduce every year. The only nonreproductive female found during this study had fat reserves of 12.1% of its body weight, which is almost twice the mean for all other female gopher snakes. Fat body cycling is much the same in male gopher snakes (Fig. 26) as it is for male western rattlesnakes. Their may be a pattern of general increase in fat reserves during the entire summer, but the ample fat bodies of most males and the high degree of individual variation makes it difficult to identify any cycles.

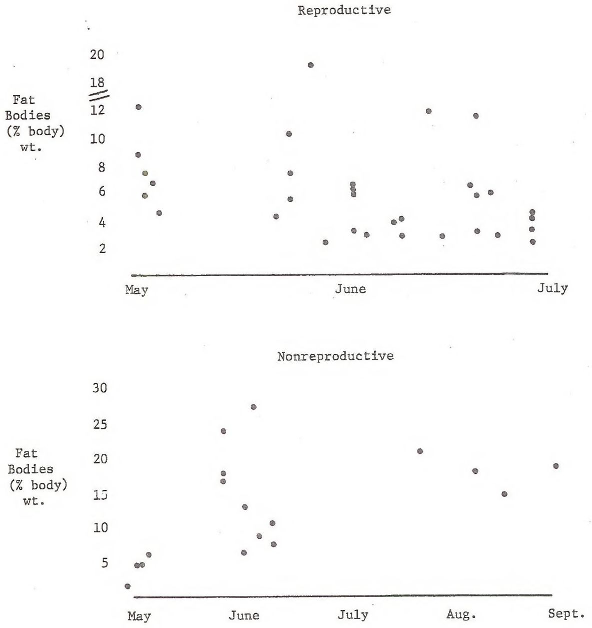


Fig. 25a. Fat Body cycles of sexually mature female western rattlesnakes.

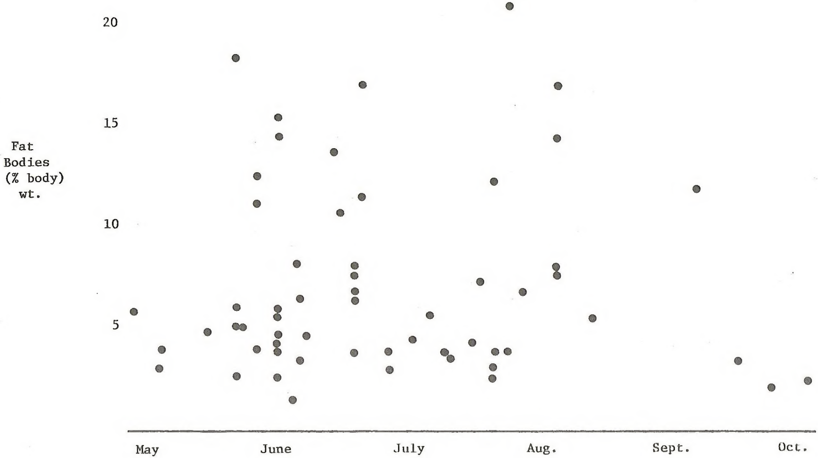


Fig. 25b. Fat body cycle of male western rattlesnakes.

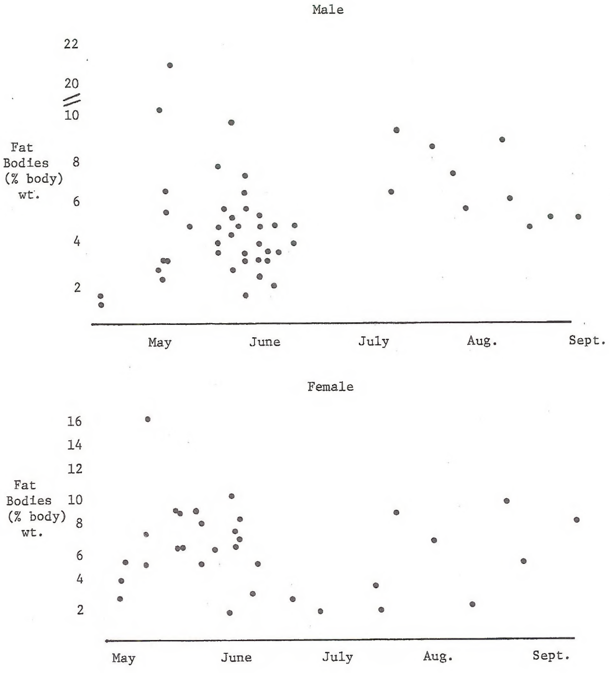


Fig. 26. Gopher snake fat body cycles.

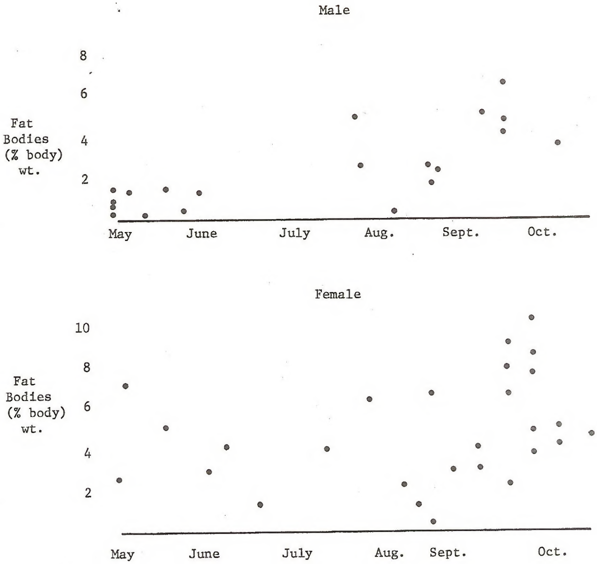


Fig. 27. Striped whipsnake fat body cycles.

Striped whipsnakes have the lowest percent body fat of the three species discussed, and in spite of smaller sample sizes, seasonal fat body cycles can be identified for both sexes (Fig. 27). Females emerge in the spring with fairly ample fat reserves, fat bodies are depleted during midsummer due to egg-laying and then build to their highest point by fall. Males emerge with their fat reserves quite depleted and remain that way throughout the spring, apparently due to breeding activity. Their fat reserves are replenished throughout the summer and reach a high point in the fall. Fat body cycles were not investigated for any other snake species in the BPSA.

Abdominal fat bodies have been found in all temperate zone snakes and lizards that have been examined, and their function is believed to be related to either over-wintering or reproduction. If the fat bodies are primarily utilized for reproduction, then females have proportionately larger fat bodies than males and there should be a decrease in fat body size during the peak of reproductive activity. If the fat bodies are primarily utilized for over-wintering, then males and females should have nearly equal sized fat bodies and the fat bodies should be smallest following spring emergence (Hahn and Tinkle 1965, and Derickson 1976). The data presented for all three snake species would indicate that fat bodies are used primarily for reproduction. However, western rattlesnakes and gopher snakes in the BPSA also appear to carry an excess of lipid reserves from year to year which have no immediate use. These lipid reserves probably function to protect the snake population from long term adverse conditions that might arise from some environmental change.

Snake food habits

Prey items of western rattlesnakes and gopher snakes are listed in Tables 21 and 22, respectively. Western rattlesnakes feed mainly on Townsend ground squirrels (Spermophilus townsendi) in the BPSA. During a four-year period (1976-1979) Townsend ground squirrels constituted more than 80% of the prey biomass ingested by rattlesnakes. This percentage would be even higher if the data from young rattlesnakes and the data from 1977 were excluded. Since Townsend ground squirrels are too large for small rattlesnakes to swallow until they have undergone several years of growth, smaller snakes feed only on small sized prey. Food habits data from 1977 reflect the

Table 21. Western rattlesnake food items. TGS = Townsend ground squirrel (*Spermophilus townsendi*), CTR = Nuttall's cottontail rabbit (*Sylvilagus nuttalli*), DM = Deer mouse (*Peromyscus maniculatus*), KR = Ord kangaroo rat (*Dipodomys ordi*) and PM = Great basin pocket mouse (*Perognathus parvus*). Minor prey species include: White-tailed antelope squirrel (*Ammospermophilus leucurus*), Desert woodrat (*Neotoma lepida*), Western whiptail lizard (*Cnemidophorus tigris*), Desert horned lizard (*Phrynosoma platyrhinos*) and Great basin spadefoot toads (*Scaphiopus intermontanus*).

Prey		1976	1977	1978	1979	Total
TGS	N	30	2	23	23	78
	biomass (g)	4524	301.6	3468.4	3468.4	11763
	% total biomass	88.6	38.0	81.2	80.4	81.2
CTR	N	2	2	3	1	8
	biomass (g)	310	310	465	155	1240
	% total biomass	6.1	39.1	10.9	3.6	8.6
DM	N	2	6	6	15	29
	biomass (g)	38	114	114	285	551
	% total biomass	0.7	14.4	2.7	6.6	3.8
KR	N	1	1	3	4	9
	biomass (g)	53	53	159	212	477
	% total biomass	1.0	6.7	3.7	4.9	3.3
PM	N	2	1	3	3	9
	biomass (g)	30	15	45	45	135
	% total biomass	0.6	1.9	1.1	1.0	0.9
minor species	N	4	0	1	3	8
	biomass (g)	148.8	----	17.8	148.8	315
	% total biomass	2.92	----	0.4	3.1	2.2
Total biomass		5104	794	4269	4314	14481

Table 22. Gopher snake food items. CTR = Nuttall's cottontail rabbit (*Sylvilagus nuttalli*), TGS = Townsend ground squirrel (*Spermophilus townsendi*), DM = Deer mouse (*Peromyscus maniculatus*), MV = Montane vole (*Microtus montanus*), KR = Ord kangaroo rat (*Dipodomys ordi*), HM = House mouse (*Mus musculus*) and PM = Great basin pocket mouse (*Perognathus parvus*). Minor prey species include: unidentified birds and eggs, side-blotched lizard (*Uta stansburiana*) and muskrat (*Ondatra zibethicus*).

Prey		1976	1977	1978	1979	Prey Totals
CTR	N	4	2	0	4	8
	biomass (g)	620	310	--	620	1550
	% total biomass	42.8	44.7	--	58.8	31.6
TGS	N	4	0	5	0	9
	biomass (g)	603	--	754	--	1357
	% total biomass	5.2	24.6	28.0	19.8	19.0
MV	N	0	2	6	2	10
	biomass (g)	--	60	180	60	300
	% total biomass	--	8.6	10.6	5.7	6.7
KR	N	0	1	2	2	5
	biomass (g)	--	53	106	106	265
	% total biomass	--	7.6	6.2	10.1	5.4
HM	N	1	5	2	0	8
	biomass (g)	17	85	34	--	136
	% total biomass	1.2	12.2	2.0	--	2.8
PM	N	0	0	2	4	6
	biomass (g)	--	--	30	60	90
	% total biomass	--	--	1.8	5.7	1.8
Minor species	N	3	1	4	0	8
	biomass (g)	134	15	120	--	269
	% total biomass	9.2	2.2	7.1	--	5.5
Total biomass		1450	694	1699	1055	4898

reduced availability of ground squirrels during a drought when squirrels entered aestivation two months earlier than usual and failed to reproduce (Johnson and Smith 1978). Fitch (1949) noted that western rattlesnakes also specialize on ground squirrels in central California. He found that 69% of their prey biomass was represented by California ground squirrels (Spermophilus beechyei). The data from my study and Fitch's work suggest that Western rattlesnakes will specialize on ground squirrels if they are available.

It should also be pointed out that this strong reliance of adult western rattlesnakes on Townsend ground squirrels was only verified for snakes north of the Snake River in the primary study area, where Townsend ground squirrels are abundant. Few food habits data were collected from the south side of the Snake River, but it is certain that rattlesnakes could not show the same prey selection there, since many areas south of the river have no Townsend ground squirrel populations at all.

Intact Townsend ground squirrels that were palpated from western rattlesnakes averaged 151 g (n - 16, range: 80-245 g). Nuttall's cottontail rabbits (Sylvilagus nuttalli) taken by rattlesnakes were in the same size range, but not enough of them were obtained to calculate a meaningful average. All cottontail rabbits taken were juveniles, which is to be expected since adult rabbits are too large to be handled by rattlesnakes in the BPSA. Smaller prey species made up an insignificant proportion of the total biomass taken by western rattlesnakes, but they are still very significant to the rattlesnake population, since the young rattlesnakes must rely on them. Small lizards may be an important prey item for young rattlesnakes. Most captive born rattlesnakes from the BPSA refused all food except small lizards during their first few months of feeding.

Gopher snakes are similar to western rattlesnakes in the BPSA in that they both feed primarily on small mammals. However, gopher snakes utilize a greater variety of prey species. They take more deer mice (Peromyscus maniculatus) than any other prey item, but because of their small body size, deer mice only represent 19% of the total biomass taken. Cottontail rabbits and Townsend ground squirrels, which make up 32 and 28%, respectively, of the total biomass taken, are the two major prey species.

Gopher snakes are capable of taking similar sized prey as is taken by western rattlesnakes. Three Nuttall's cottontail rabbits and three Townsend ground squirrels palpated from gopher snakes ranged in size from 90 to 200 g ($\bar{x} = 136$). Because gopher snakes are smaller in body size than western rattlesnakes, but often take similar sized prey, gopher snakes tend to ingest larger prey items relative to their body size than do rattlesnakes. Western rattlesnakes typically did not take prey larger than one-third to one-half their own body weight, while gopher snakes would take prey that was half their own body weight or more. One gopher snake was found that had recently ingested five deer mice with a combined weight which exceeded the snake's weight. However, gopher snakes were also sometimes found with one or more neonates of a prey species in their stomachs, indicating they will also injest very small prey items.

Few food habits data were gathered for striped whipsnakes, but even with limited data, it is apparent that they are very generalized feeders. No one prey species was predominant in either numbers taken or biomass ingested. They also did not appear to have a preference in the class of prey taken. Some of the prey taken by striped whipsnakes in the BPSA were: two species of mice, three species of lizards, two species of frogs, a neonate bird, an unidentified species of bat and other snakes. Food habits data were not gathered for any other snake species in the BPSA.

Consumption Rates and Growth Efficiency of Snakes

The results of feeding studies done with western rattlesnakes and gopher snakes are given in Table 23. In both species of snake, juveniles had higher consumption rates and growth efficiencies than the combined older age classes. The differences in growth efficiencies are not statistically significant ($\alpha = 0.05$) because of the high variance and small sample sizes, but we believe the differences are biologically meaningful. No significant differences could be found between the sexes, and these values were not included in Table 23. It is possible that differences do occur between the sexes, but the sample sizes were too small to identify them.

Western rattlesnakes had higher consumption rates and greater growth efficiencies than gopher snakes in all categories, although only the combined estimates showed a statistically significant difference. Rattlesnakes appear to be less active compared to gopher snakes, and thus would use less energy on activity. Assuming rattlesnakes have a assimilation efficiency similar to gopher snakes, they would have a greater percentage of their

Table 23. Consumption rates and growth efficiencies of captive western rattlesnakes and gopher snakes. Consumption rate is expressed as a percentage of the snakes body weight that is consumed per day. Growth efficiency is defined as the total increase in snake body weight divided by the total weight of prey ingested times 100.

Snake	Consumption rate			Growth efficiency		
	n	$\bar{x}$	SD	$\bar{x}$	SD	
Western rattlesnake						
juveniles	11	3.0	1.06	30.0	7.34	
all others	20	1.6	0.54	27.6	8.17	$t = 0.81$
combined	31	2.1	0.98	28.5	7.85	
Gopher snakes						
juveniles	10	2.2	0.62	23.6	3.81	
all others	33	1.5	0.83	20.4	6.58	$t = 1.5$
combined	43	1.7	0.84	21.2	6.15	

ingested prey available for some form of tissue production (including reproduction), and thus would have a greater growth efficiency. There does not seem to be an intuitive explanation for western rattlesnakes having a higher consumption rate than gopher snakes. In fact, it would seem more logical for the more active and energetic species to have the greater consumption rate. It is always possible that it is merely an artifact of the captive environment.

One might expect that there would be a correlation between consumption rate and growth efficiency in a feeding study like this. If the energy for maintenance and activity stayed fairly constant, then the more a snake ate, the greater the percentage of total energy left for growth. However, when growth efficiency was regressed against consumption rate, there was no significant correlation ($r = 0.09$ and -0.03, respectively, for western rattlesnakes and gopher snakes). Assimilation efficiency may decrease with increased consumption rate to offset any potential increase in growth efficiency.

Consumption rate was estimated in this study by using a direct approach and by doing feeding studies. It can also be estimated by an indirect approach based on energetics. To provide an independent check on the reliability of our consumption rate estimates, Chuck Peterson at Washington State University, who specializes in energetics and thermal ecology of snakes, calculated consumption rates for western rattlesnakes and gopher snakes based on energetics. He used estimates from the literature on assimilation efficiency, standard and active metabolic rates, and estimates from this study on activity, thermal regimes, reproduction and growth. This indirect estimate of consumption rate was 21% lower than the direct estimate for western rattlesnakes and 25% higher for gopher snakes. (Considering the lengthy calculation and the number of assumptions involved in deriving this second estimate, the two estimates are remarkably close and tend to verify the validity of our original estimates of consumption rates.) Ironically, the indirect estimates of consumption rates indicate that gopher snakes have a higher consumption rate than western rattlesnakes, which actually seems to fit better with the general nature of these two snake species as described earlier.

Impact of Western Rattlesnake and Gopher Snakes on Mammalian Prey Species

Since most rattlesnakes with food in their stomachs were found from late April until the end of July, it was estimated that these snakes feed for about 100 days each year. Multiplying 100 days of feeding by the daily consumption rate (Table 23) gives annual consumption rates of 1.6 and 1.5 times the body weight, respectively, for western rattlesnakes and gophers snakes. Using a mean body weight of 401 g for western rattlesnakes and 218 g for gopher snakes yields mean annual consumption estimates of 661 and 328 g of prey ingested, respectively, for an average western rattlesnake and gopher snake. Since food habits are known, annual consumption can be broken down into the average number of each prey species taken (Table 24). Finally, density estimates for these two snake species can be used to estimate the mean number of each prey species taken per hectare in the BPSA (Table 25).

Although the estimates in Table 25 are somewhat rough, we feel that they do illustrate the potential impact of western rattlesnakes and gopher snakes on mammalian prey species in the BPSA. Because of their generalized diet, gopher snakes are not likely to have a significant impact on any one prey species. Gopher snakes are also quite ubiquitous in the BPSA, but are nowhere concentrated in high density, so that they are not likely to have even a localized impact on prey species. In contrast, western rattlesnakes have a selective diet and are more likely to have a significant impact on their preferred prey species, the Townsend ground squirrel. Rattlesnakes also have a patchy distribution in the BPSA, and in certain areas of preferred habitat they occur in very high densities. In these localities it is almost certain that they would have a significant impact on Townsend ground squirrels. The estimate of 25 Townsend ground squirrels consumed per hectare by rattlesnakes in areas of maximum snake density seems unrealistically high, since Townsend ground squirrels seldom occur anywhere in such high densities (USDI 1979). We believe that this consumption estimate is reasonable and merely indicates that rattlesnakes disperse out from these areas of maximum snake density to feed. The impact of western rattlesnakes on Townsend ground squirrels can best be summed up by saying that in and around scattered areas of high rattlesnake density a high percentage of the annual production of squirrels is removed by rattlesnakes, but in most other areas the impact would only be slight.

Table 24. Annual number of prey ingested by an average western rattlesnake and gopher snake.

Prey Species	Percent in diet	Grams ingested	Number of Individuals
Western rattlesnake			
Townsend ground squirrel	81	537	3.6
Nuttall's cottontail rabbit	9	57	0.4
Deer mouse	4	25	1.3
Ord Kangaroo rat	3	22	0.4
Great basin pocket mouse	1	6	0.4
Others	2	14	---
Total Consumption		661 g	
Gopher snake			
Nuttall's cottontail rabbit	32	104	0.7
Townsend ground squirrel	28	91	0.6
Deer mouse	19	62	3.3
Montane vole	6	20	0.7
Ord kangaroo rat	5	18	0.3
House mouse	3	9	0.5
Great Basin pocket mouse	2	6	0.4
Others	5	18	---
Total Consumption		328 g	

NOTE: Based on a mean body weight of 401 g for western rattlesnakes and 218 g for

Table 25. Annual number of prey consumed per hectare by western rattlesnakes and gopher snakes.

Prey Species	$\bar{x}$ snake density (0.6 snakes/ha)	Maximum density (6.9 snakes/ha)
Western rattlesnake		
Townsend ground squirrel	2.3	24.7
Nuttall's cottontail rabbit	0.2	2.6
Deer mouse	0.8	9.1
Ord kangaroo rat	0.2	2.6
Great basin pocket mouse	0.2	2.7
	(1.3 snakes/ha)	(1.9 snakes/ha)
Gopher snake		
Nuttall's cottontail rabbit	0.9	1.3
Townsend ground squirrel	0.8	1.2
Deer mouse	4.1	6.1
Montane vole	0.8	1.2
Ord kangaroo rat	0.4	0.6
House mouse	0.6	1.0
Great basin pocket mouse	0.5	0.7

The notion that a rattlesnake could be a significant predator on ground squirrels is not totally without precedence. Based on a long term study in central California, Fitch (1948) estimated that western rattlesnakes were the major predator on California ground squirrels (*Spermophilus beecheyi*). He estimated the rattlesnake density at about one snake per acre (about 2.5 snakes/ha) and snake consumption at two times the snakes' weight annually, with 69% of their diet made up of ground squirrels. This population of rattlesnakes removed an estimated 34% of the annual production of ground squirrels.

Two variables which are difficult to estimate could influence the impact that these two snake species have on mammalian prey. First gopher snakes have a tendency to "raid" nests of small mammals and consume all of the young. The percentage of a gopher snake's diet made up of these young is certainly going to be underestimated, since mammalian young are more difficult to detect and palpate from the stomachs of gopher snakes. These young also lack hair, so they are completely missed in the analysis of snake scats. The impact of gopher snakes on their prey species would certainly be much greater than previously estimated if a substantial proportion of their diet is made up of neonates.

The second variable is prey waste by rattlesnakes. In the same study mentioned above, Fitch (1948) states that many California ground squirrels struck by western rattlesnakes wander too far before dying and are not recovered. In our captive feeding studies, prey were sometimes struck by rattlesnakes and immobilized almost immediately, while other times they remained mobile for up to 30 minutes before dying. It seems very likely that many of the envenomated prey that remain mobile for even several minutes in a natural setting would travel too far to be recovered by the rattlesnake that struck them. This was never directly witnessed in the field, but on several occasions Townsend ground squirrels were found dead in areas of high rattlesnake density, although they were always too decomposed to determine cause of death. Also, a radioactively tagged rattlesnake searched the same general area for almost two days before it found a badly decomposed cottontail rabbit and proceeded to swallow it. It seemed apparent that the rattlesnake had initially struck the rabbit, which had run off some distance and died, and the rattlesnake had fortuitously found it after many hours of searching (see Appendix B). Anyway, there is no doubt that rattlesnakes do waste some proportion of their prey, which would increase their impact on the prey by an unknown amount.

Response of western rattlesnakes and gopher snakes to prey availability

During a normal year, Townsend ground squirrel young emerge from late March to early April and are active above ground until mid-June to mid-July. These juvenile squirrels are subject to western rattlesnake and gopher snake predation from late April until they enter torpor in July. However, a drought during winter 1976 and spring 1977 caused the Townsend ground squirrels in native vegetation to fail to reproduce, and all squirrels entered torpor by mid-May (USDI 1979). Thus in 1977, only adult Townsend ground squirrels were available as snake prey for several weeks in spring and none of the juveniles, which are the usual prey of these snakes, were present. The manner in which western rattlesnakes and gopher snakes responded to this loss of a major prey species is significant in understanding their respective ecologies.

The effect that the loss of a major prey species had on food habits of western rattlesnakes and gopher snakes can be seen in Table 26 and Figs. 28 and 29. Western rattlesnakes showed an almost 80% reduction in relative prey consumption in 1977, which is about equal to the proportion that Townsend ground squirrels make up in their diet. This would indicate that there was no shift to alternate prey species, and apparently most of these rattlesnakes will not feed if they cannot find their preferred prey. After 1977, rattlesnakes returned to their usual food habits and consumption rates.

The effect of this prey loss on gopher snakes is more difficult to interpret. They showed a 60% reduction in relative prey consumption in 1977, but the consumption rate stayed almost as low in 1978 and 1979. It does not seem reasonable that the drought in 1977 would have such a lasting effect on food habits of gopher snakes. Rattlesnakes did not show this long term effect, and other aspects of gopher snake biology, which will be discussed later, give no indication that their prey consumption has been reduced. It seems more likely that the sample of food habits from 1976 over estimated their actual consumption for that year. This could result from two factors. First, relative prey consumption was adjusted to be the amount of prey identified per 100 snakes captured, and in 1976 only 61 gopher snakes were collected, which was about one-half the average number captured for the remaining three years. This small sample size would magnify any error in

Table 26. Incidence of palpable prey found in western rattlesnakes and gopher snakes at time of capture.

	Western rattlesnakes			Gopher snakes		
	Snakes with palpable prey	Total Captures	%	Snakes with palpable prey	Total captures	%
1976	19	110	17.3	6	61	9.8
1977	5	77	6.5	3	73	4.1
1978	13	72	18.1	7	155	4.5
1979	15	64	23.4	3	95	3.2

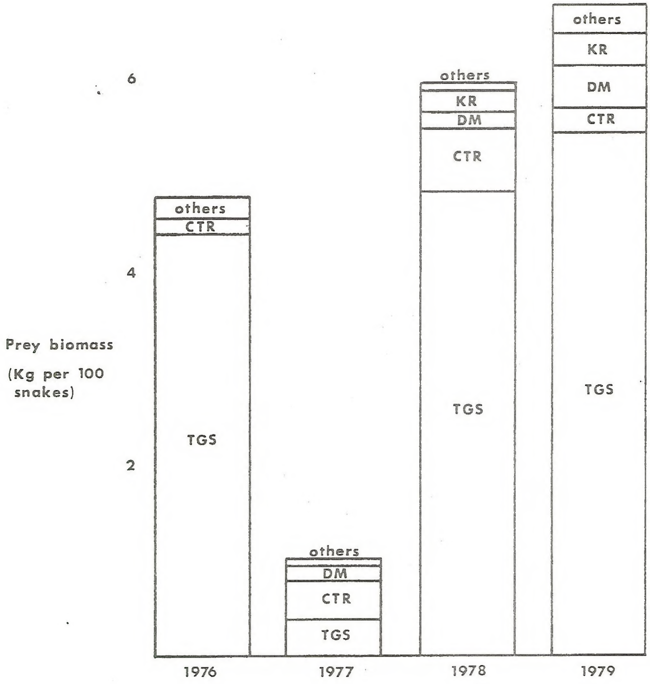


Fig. 28. Annual variation in western rattlesnake food habits. TGS = Townsend ground squirrel, CTR - Nuttall's cottontail rabbit, DM = deer mouse and KR = Ord kangaroo rat.

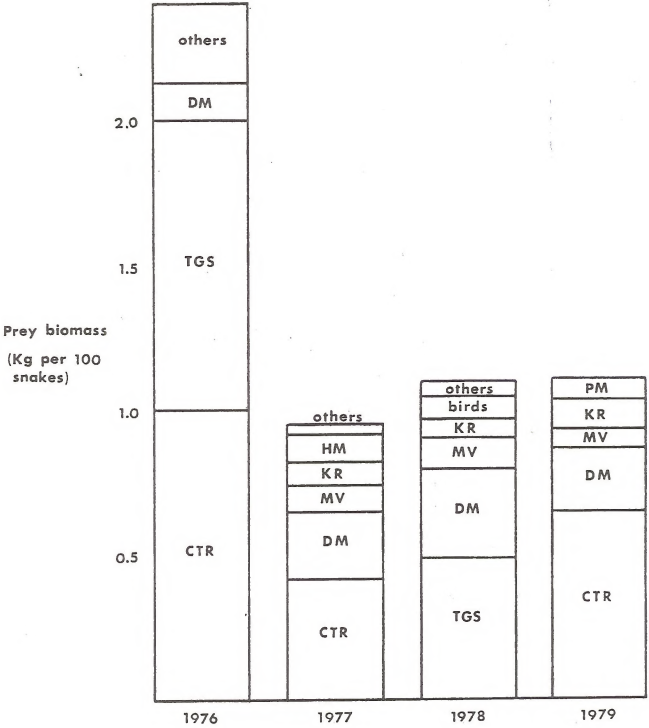


Fig. 29. Annual variation in gopher snake food habits. CTR = Nuttall's cottontail rabbit, TGS = Townsend ground squirrel, DM = deer mouse, MV = montane vole, KR = Ord kangaroo rat, HM = house mouse and PM = Great Basin pocket mouse.

estimating relative consumption rates. Second, 84% of the total prey biomass taken in 1976 by gopher snakes came from Townsend ground squirrels and cottontail rabbits. This is much higher than any year after that time. If by chance a high percentage of the gopher snakes collected in 1976 had recently fed on one of these two prey species, it would greatly increase the total annual consumption, since ground squirrels and cottontail rabbits have a much greater biomass than any of the other prey species. I conclude that the relative consumption rate for gopher snakes may have been higher in 1976 than any following year, but the difference is not as great as it would appear from Fig. 29. This would mean that there was not a dramatic decrease in prey consumption in 1977 relative to all other years, although no Townsend ground squirrels showed up in the diet of gopher snakes that year.

The relative effect of the drought and the loss of a major prey species on western rattlesnakes and gopher snakes is also evident in other ways. As seen in Fig. 30, seasonal activity of western rattlesnakes changed dramatically in 1977. In a normal year, as seen by the combined 1975 and 1976 seasons, activity decreases over the summer, but there is at least some activity until fall. In 1977, almost no rattlesnakes could be found by the end of June. Rattlesnake activity also dropped off somewhat early in 1978, but appeared normal in 1979. There was no such early disappearance of gopher snakes seen in 1977 (Fig. 31). Gopher snakes did not show as high a peak of activity in 1977 as usual, but their activity continued throughout the summer like a normal year. Seasonal activity for 1978 and 1979 was not included in Fig. 31, since all years were very similar.

The regression of body weight on snout-vent length will give an equation indicating the relative heavy bodiedness of a snake. If two groups of snakes of the same species are compared, the heavier or more robust group would yield a regression line above the regression line from the thinner snakes. This regression was done for western rattlesnakes and gopher snakes to see if there was any indication that the snakes became somewhat emaciated as a result of the prey loss in 1977 (Figs. 32 and 33). The relationship between body weight and snout-vent length is not linear, so body weight was transformed to the cube root of the weight. This produced the most linear regression of any transformation, but it makes the relative difference between regression lines look smaller. In spite of this, the slope of the regression for the combined years of 1975 and 1976 is significantly greater

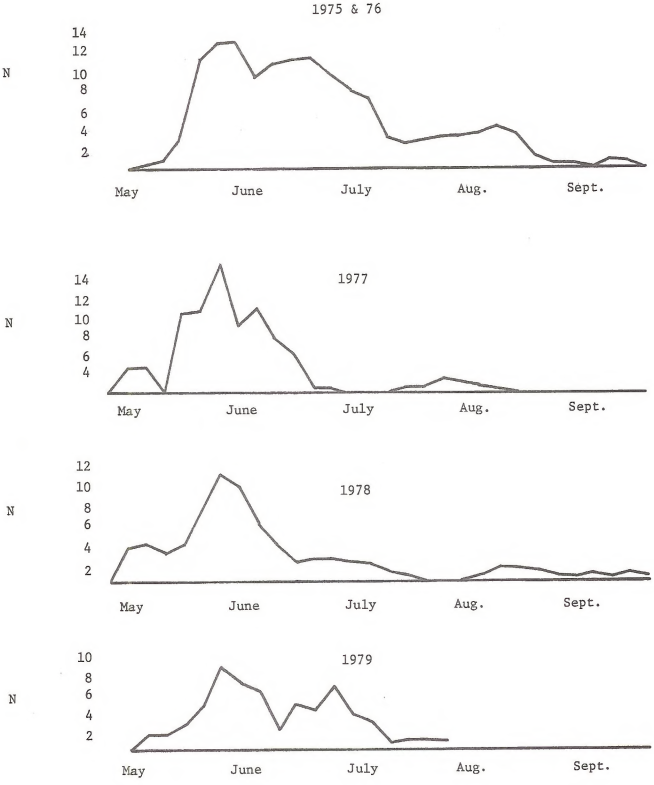


Fig. 30. Seasonal activity of western rattlesnakes as indicated by frequency of captures from 1975 to 1979.

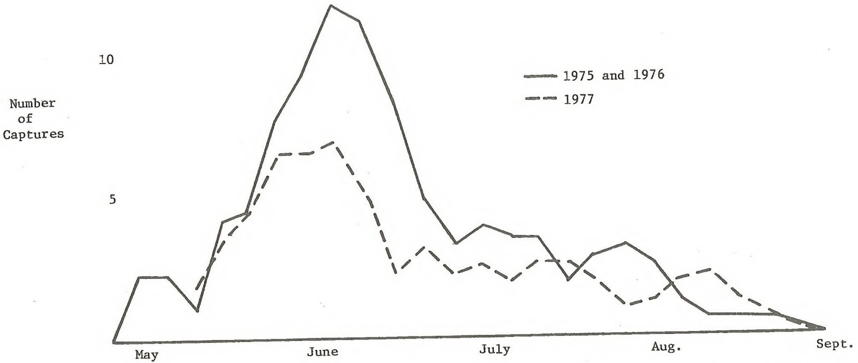


Fig. 31. Seasonal activity of gopher snakes as indicated by frequency of captures from 1975 to 1977.

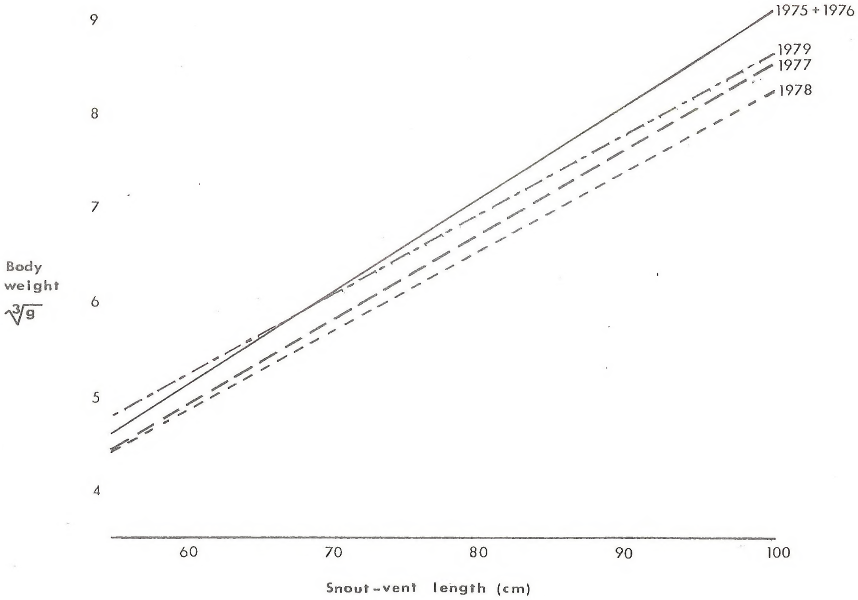


Fig. 32. Regression of body weight on snout-vent length for western rattlesnakes.

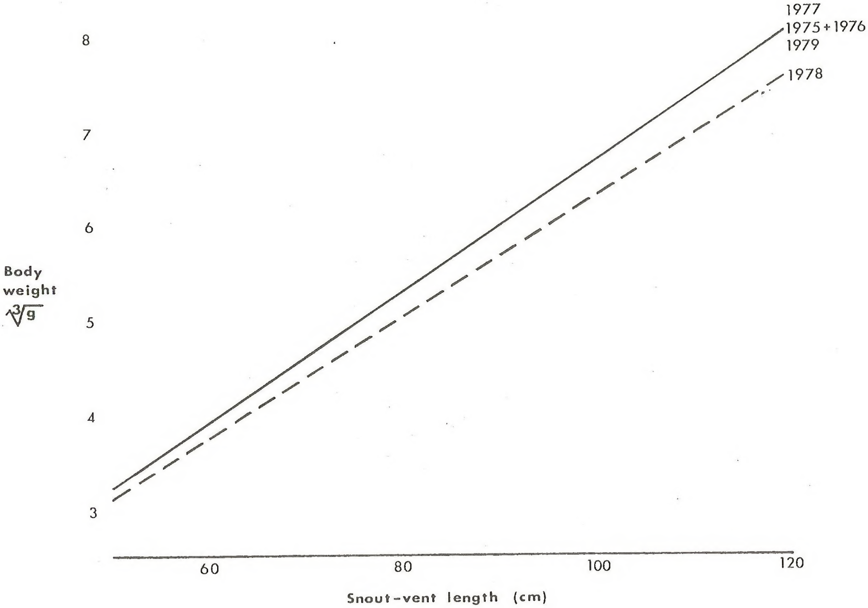


Fig. 33. Regression of body weight on snout-vent length for gopher snakes.

($P < 0.001$) than any of the following years. The regression from 1978 produced the lowest slope, indicating the rattlesnakes were the most emaciated the year after the drought year. As indicated by the regressions, rattlesnakes were again heavier in 1979 than either 1977 or 1978.

Gopher snakes did not show as much fluctuation in body weight due to the drought as compared to rattlesnakes. There was no change in the regression of body weight on snout-vent length in 1977 relative to 1975 and 1976. Only snakes from 1978 produced a regression line below the pre-drought snakes, indicating that gopher snakes were slimmer in that one year.

Recapture data also indicates that the major weight loss in western rattlesnakes due to the 1977 drought occurred in 1978. Eight out of ten adult male rattlesnakes lost an average of 54 g in 1978 over their previous year's weight. (Females were excluded because their reproductive condition can confuse weight loss and gain.) Only three males captured in 1978 were recaptured in 1979, but of these, all gained weight in 1979. Gopher snakes were too infrequently recaptured to provide much insight into weight changes, but three males captured in 1977 all showed weight gain in 1978.

Sample sizes were too small and individual variation too high to use yearly changes in mean fat body size as an indication of snake condition. However, it would appear that rattlesnakes had a higher percent body fat in 1975 and 1976, than they did in any subsequent year, although the differences were not statistically significant. No gopher snakes were analyzed for fat body condition prior to 1978, so no comparisons can be made with them.

Probably the most significant effect of the drought and the loss of a major prey species on western rattlesnakes was the decrease in reproduction (Table 27). The percent of mature female rattlesnakes that were reproductively active each year dropped from about 75% in 1976 and 1977 to only 33% in 1978. In 1979 the reproductive rate jumped to 87% and then apparently returned to a normal 75% in 1980. No reproductive data were collected for gopher snakes before 1978, but the reproductive rate was nearly 100% from 1978 to 1980 (Table 27). There is no indication that the drought affected gopher snake reproduction.

The apparent response of western rattlesnakes to the loss of their principal prey species can be summed up as follows: when most rattlesnakes were unable to find their preferred prey item in the spring of 1977, they

Table 27. Percent mature female western rattlesnakes and gopher snakes reproductive each year.

	Western rattlesnake		Gopher snake	
Year	Gravid/Total	%	Gravid/Total	%
1976	14/19	74	--	--
1977	8/11	73	--	--
1978	5/15	33	13/13	100
1979	20/23	87	10/10	100
1980	6/8	75	7/8	88
TOTAL	53/76	70	30/31	97

simply did not feed. After being active for a short time in the spring, most of these same snakes went back into hibernation (or aestivation). This would be an apparent adaptation to minimize the prolonged effects of fasting. Females that emerged in the spring of 1977 with sufficient fat reserves to reproduce that year could proceed and have young, since they seldom feed when gravid (or pregnant) anyway. The greatest impact of the drought was seen the following year. Rattlesnakes were in relatively poor condition in 1978, since many snakes had fasted or had fed only a limited amount since the summer of 1976. (Based on captive feeding experiences from this study and numerous references, it is easily possible for healthy rattlesnakes to fast for such a period of time, especially if they are in a hibernating/aestivating condition most of this time.) Because of their low fat reserves most females were unable to reproduce in 1978. However, since the majority of females were nonreproductive in 1978 and spent that summer replenishing fat reserves, there was a higher than usual percentage of females that were able to reproduce in 1979. By 1980, rattlesnakes in the BPSA should have been back to a normal pre-drought condition.

Rattlesnakes appear to have a very successful ecological adaptation to the environment found in the BPSA. They are able to specialize on a particularly ideal prey species, and they have large fat reserves, which they can behaviorally conserve, so that they are able to survive dramatic flucuations in their prey population. However, a long term decline in their preferred prey could result in a decline in the rattlesnake population and a gradual shift to other prey species.

There is circumstantial evidence that would also support the close tie between western rattlesnakes in the BPSA and their preferred prey species the Townsend ground squirrel. In 1975, an area near "Tom Draw" was established to do a mark-recapture study of rattlesnakes. During that summer, 14 rattlesnakes were marked (density estimated = 5.6 snakes/ha), and Townsend ground squirrels appeared very abundant. The next year (1976) only 5 rattlesnakes were captured all summer, and there appeared to be a noticeable absence of ground squirrels in the area. No rattlesnakes were found in this area in 1977. There were also no ground squirrels seen in the area that summer. (Of course, the drought caused ground squirrels to appear scarce everywhere in 1977.) In 1978 ground squirrels seemed fairly abundant again in this mark-recapture study area, and three rattlesnakes marked in 1975 were found. Two of these rattlesnakes had not been seen since 1975, and they were in the same precise location where they had been originally captured. This seemed to suggest that something had caused the Townsend ground squirrel to decline in this one area (possibly from a local disease outbreak or even local rattlesnake predation) and rattlesnakes had dispersed to find areas of higher ground squirrel density. Then after the local ground squirrel population began to rebuild, these same rattlesnakes began to return to their original location.

Gopher snakes have adapted a different ecological strategy to cope with prey fluctuations. They simply have a very broad prey base, so that the reduction of one prey species will have little impact on their total prey consumption. Thus, the loss of Townsend ground squirrels in 1977 appeared to have no significant impact on gopher snakes. The more generalized food habits of gopher snakes probably also explains their more ubiquitous distribution in the BPSA. However, the gopher snakes' inability to specialize on a particularly ideal prey species might explain why they do not have areas of high densities as do rattlesnakes.

Possible effects of habitat alteration on reptile densities

The effects of habitat alteration on lizard and snake densities in the BPSA can be predicted from their habitat preferences. In general, lizards require open ground with only scattered vegetation. Thus grazing activity might actually benefit lizard populations in some cases (Reynolds 1979), but any type of cultivation would virtually eliminate all lizards.

It is more difficult to predict the response of snake populations to habitat alterations. In general, snakes require some type of cover in the form of rocks, rodent burrows or dense vegetation, and an appropriate prey base. Grazing activities are not necessarily beneficial or deleterious to most snake species. Cultivation has a very negative impact on most snake species, because it removes the natural cover and alters the prey base. Some snake species such as gopher snakes may appear superficially to benefit from cultivation due to the tendency of certain rodents to be attracted to some agricultural crops. However, the snakes are restricted to the edge of such cultivated areas, since they must return to noncultivated areas for cover. Cultivation is particularly deleterious to rattlesnakes, since it also results in high human predation, which is probably the main cause of mortality for adult rattlesnakes.

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Appendix A Miscellaneous vertebrates captured in drift fences. Rip. = riparian; tal. = talus; shad. = shadscale; B.S. = Big Sage; W.F. = winterfat.

	Drift Fences												
Species	rip. (a)	rip. (b)	tal. (a)	tal. (b)	rim (a)	rim (b)	shad. (a)	shad. (b)	B.S. (a)	B.S. (b)	W.F. (a)	W.F. (b)	SPECIES TOTALS
AMPHIBIANS													
Pacific treefrog	65	--	10	1									76
Great Basin spade-foot toad	22	8	3	4		2				3			42
Woodhouse's toad	21	1	11										33
REPTILES													
Side-blotched lizard			6	2			2	5			2		17
Western whiptail lizard		3	1		2		8		7	1			22
Western fence lizard			1	4	1								5
Leopard lizard							3	1		4			8
Desert horned lizard							4						4
MAMMALS													
Deer mouse	3	3		2	2	3	1	1	4	3	1	2	25

Appendix A (continued)

Species	Drift Fences rip. (a)	rip. (b)	tal. (a)	tal. (b)	rim (a)	rim (b)	shad. (a)	shad. (b)	B.S. (a)	B.S. (b)	W.F. (a)	W.F. (b)	SPECIES TOTALS
MAMMALS													
Desert woodrat	20		7					1					28
Bushy-tailed woodrat	1	2		1			2						6
Ord's kangaroo rat	2	1				1	1		2	1		4	12
Ord's pocket mouse		2								1			3
Townsend ground squirrel												1	1
Spotted skunk	1		1										2
Townsend pocket gopher	1												1
Montane vole				1									1
BIRDS													
Canyon wren						9							9
Sage sparrow										1			1
Drift Fence Totals	136	20	40	15	5	15	21	8	13	13	3	7	296

Appendix B. Summary of observations made on radioactively tagged snakes in the BPSA.

Crotalus viridis #620, adult non gravid female, captured 20 May 1979 near the canyon rim.
24 May released, 30 May relocated 76 m NNE of release site,
30 May - 10 June (12 days) remained in the same location either under or near a large flat rock located next to the canyon rim
11 June has moved
12 June located 98 m N under a flat rock at the canyon rim - has begun ecdysis
13 June has moved
19 June relocated 48 m 55 w under rocks
27 June ecdysis completed
19 - 29 June (11 days) remained in same location always under the rocks
30 June has moved - never relocated

Crotalus viridis #644, adult gravid female, captured 27 May 1979 in grass/sandy area
30 May released, 31 May relocated 7 m NE in a kangaroo rat burrow
1 June has moved
5 June 1300 hrs relocated 11 m NNE in a kangaroo rat burrow
5 June 2000 hrs has moved
8 June relocated 30 m NW in a kangaroo rat burrow
9 June has moved
11 June relocated 135 m NW beneath a saltbush
19 June has begun ecdysis
11 - 24 June (14 days) remained in same location either under brush or in a kangaroo rat burrow
24 June moved off in a northerly direction - never relocated

Crotalus viridis #668, adult male, captured 6 June 1979 near the canyon rim
8 June released, 9 June relocated 143 m N under rocks - has begun ecdysis
9 - 20 June (12 days) remained in same location under rocks
21 June has moved - never relocated

Crotalus viridis #698, adult male, captured 7 July 1979 in greasewood/sandy area
8 July released, 9 July 0900 hrs relocated 30 m N in white-tailed antelope squirrel burrow
9 July 2100 hrs relocated 12 m NNW in open next to a kangaroo rat "run"
10 July 0930 hrs relocated 54 m N in big sage
10 July evening - 12 July 1000 hrs snake was in the same area making repeated forays of 25-30 m out from a central focus in a NE to SE quadrant
12 July 1000 hrs snake locates and ingests a decaying cottontail rabbit that was found in the SE corner of its searching quadrant
13 July relocated 10 m W in a white-tailed antelope squirrel burrow
13 - 17 July (5 days) remains in same location in the burrow
18 July has moved
19 July relocated 17 m NW in a white-tailed antelope squirrel burrow - has regurgitated part of the cottontail rabbit
23 July has moved - never relocated

Crotalus viridis #621, subadult male, captured 20 May 1979 in shadscale
30 May released - went down a Kangaroo rat burrow
31 May remained in the same location
1 June has moved - never relocated

Crotalus virdis #688, adult male, captured 25 June 1979 in cheatgrass/sandy area
7 July released - never relocated

Crotalus viridis #689, adult male, captured 25 June 1979 near the canyon rim
7 July released - travelled 42 m NW and went under a rock near the rim
8 July has moved - never relocated

Pituophis melanoleucus #648 and 649, both adult males, captured 27 May 1979 in big sage and shadscale, released 30 May and never relocated

Pituophis melanoleucus #662 & 677, adult males, captured 1 June and 13 June 1979 respectively in greasewood; released 5 and 20 June respectively and were followed on the surface for two hours (the distance they travelled was not measured) until they disappeared down rodent burrows and were never relocated.

Pituophis melanoleucus #664, adult male, captured 4 June 1979 in sandy/grass area
5 June released snake and followed it for one hour, it went down one kangaroo rat burrow immediately upon release, re-emerged and travelled 52 m in an arc where upon it entered another burrow, disappeared out of monitoring range and was never relocated

Pituophis melanoleucus #666, adult male, captured 7 June 1979 in a sandy/grass area
8 June released snake where upon it immediately entered a kangaroo rat burrow
8 - 21 June (14 days) in same exact location 33 cm below the surface in the burrow
22 June snake emerged from burrow, shed skin and disappeared - never relocated

Pituophis melanoleucus #679, adult male, captured 19 June 1979 in greasewood
20 June released snake and followed it on the surface for two and one half hours, it travelled 55 m in a tight arc and went down a kangaroo rat burrow where it could still be monitored underground for 20 minutes and then it disappeared out of monitoring range without re-emerging - never relocated

Pituophis melanoleucus #697, adult male, captured 6 July 1979 in greasewood
8 July released snake; it travelled 10 m and went down a white-tailed antelope squirrel burrow; it could be monitored underground for two hours, then disappeared without re-emerging - never relocated

Pituophis melanoleucus #700, juvenile female, captured 12 July 1979 in sandy/grass area
16 July released snake and lost contact in 10 minutes down a rodent burrow

Hypsiglena torquata #10, adult male, captured 20 May 1979 in greasewood
- 30 May released, 31 May relocated 12 m NNE in a white-tailed antelope squirrel burrow
- 31 May - 2 June remained in same location, then moved and was never relocated

Hypsiglena torquata #602, adult male, captured 18 May 1979 near the canyon rim
- 24 May released snake; it travelled 10 m and burrowed in debris at the base of a big sage
- 25 May snake has moved and was never relocated

Hypsiglena torquata #671, adult gravid female, captured 10 June 1979 near canyon rim
- 11 June snake released and disappeared in a rocky area and could not be relocated
- 6 July recaptured 35 m S in a drift fence and released again at the original release point - once again it disappeared and could not be relocated

Rhinocheilus lecontei #642 and 646, adult female and male, captured 39 May 1979 in greasewood and big sage respectively; released 30 May and never relocated

Masticophis taeniatus #699, subadult female, captured 12 July 1979 in sandy/grass area
- 16 July snake released and followed for 45 minutes, it travelled 65 m in an erratic arch before entering a rodent burrow - could be monitored in the burrow for 24 hours then disappeared - never relocated

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